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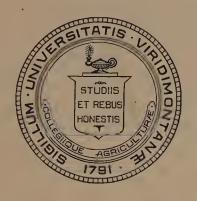
University of Vermont and State Agricultural College

Vermont Agricultural Experiment Station

BURLINGTON, VERMONT

SOME NATURAL VIOLET HYBRIDS OF NORTH AMERICA

By EZRA BRAINERD



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BULLETIN 239: SOME NATURAL VIOLET HYBRIDS OF NORTH AMERICA

By Ezra Brainerd

CONTENTS

I.	Introduction	3- 5
11.	Some Natural Violet Hybrids	6-201
III.	Index to Bulletins 224 and 239	202-204

I. INTRODUCTION

By George P. Burns

The Vermont Station presents herewith the results of the field and experimental studies of Brainerd on natural violet hybrids which have been found growing in the wild. The plants studied have been collected by or sent to him during the past 28 years by his numerous correspondents from all parts of the United States and some provinces in Canada. These have been transplanted to his garden in Middlebury, Vermont. At one time "his collection contained approximately 3,500 plants of 650 different numbers, some 200 of which were from the wild and 450 raised from seed."

These plants grew profusely and flowered naturally. He raised seedlings from the seeds of cleistogamous flowers and studied the progeny. The results of this critical analysis of his plants showed that many of them segregated and in this bulletin he describes 82 hybrids. While the new forms arising from his natural hybrids may show, in general, a separation in accordance to Mendelian principles he never found an example of pure segregation of characters. The offspring always showed to a greater or less extent a blending of the characters of the parents.

From his observation of the freedom with which violets cross under natural conditions, Brainerd came to the conclusion that the limit of hybridization in this genus is set only by the lack of cohabitation of the different species.

The climate, topography and soil conditions in Vermont offer a maximum number of plant habitats and an exceedingly rich field for the ecologists. Nevertheless the fact that such a large number of hybrids of both Rubus and Viola have been described from Vermont is not so much due to these natural conditions as to the fact that in Brainerd she has one of our keenest botanists who has devoted lavishly both his time and money to an intensive study of these two genera. When one studies the various papers and maps dealing with plant distribution, one often wonders if they are not maps showing the distribution of botanists rather than of plants. The vacant places may be due, at least in part, to the absence of botanists rather than to the lack of plants.

The range of possible crossing and, hence, possible hybridization among violets is being tested at this Station by Mr. A. Gershoy. He is making a synthetic study of the possibility of producing hybrids among the violets in the greenhouse and experimental gardens. A dctailed account of these genetic and cytological studies will be published shortly in a station bulletin.

Of the 82 natural hybrids listed and described in this bulletin Mr. Gershoy has already synthesized 20 in cultures started in 1921 at Columbia University and transferred here in 1923. In addition, he has made 61 other species crosses. Reciprocal crosses have likewise been made in the case of 30 out of his total of 81 species crosses, and 30 of these represent intersectional hybrids; as, for example:

			_
Female parent		M	ale parent
V. conspersa	X	V.	pallens
V. conspersa	\times	V.	rugulosa
V. pallens	X	V.	cucullata
V. pallens	X	V.	tricolor
V. primulifolia	X	V.	canadensis
V. sororia	X	V.	odorata

Another interesting hybrid was obtained by using for the female a hybrid obtained by crossing V. pallens female and V. lanceolata male with pollen from V. striata.

A consideration of the behavior of Rubus and Viola as revealed in the studies carried out at this Station shows the vast amount of material—new individuals—which are constantly arising and from which natural selection may determine those fit to survive. Of the numerous new individuals thus arising only those few will survive which accidentally fall in habitats in which physical conditions are suited for their development. On the other hand the variation may be such that the individuals could not survive in any habitat.

In hybridization followed by a recombination in which the offspring form a graded series between the parental types, but probably never identical with either, we have a method of mixing two variable protoplasms and from this mixture obtaining a large number of variants. The impact of the environment does not change the composition but only makes it possible for its various elements to express themselves morphologically and, hence, to become capable of description and usable in systematic work. The impact of the environment cannot be the cause of the origin of new species. If the plant is able to respond morphologically and physiologically to an environment in such a way that nothing conflicts with its ability to go through its entire cycle of development from seed to seed, it is then said to be adapted to that habitat. Adaptation is then only a negative factor.

It would seem from this work of Brainerd, as well as from that of others, that the only possible conception of species formation that the evolutionary taxonomist can accept is a dynamic one. New distinct forms have arisen in the past and are constantly arising; and those which are capable of adapting themselves to the habitat into which they have accidently fallen may prove to be new species. This involves primarily a relationship to the species which had been previously established, for, as Hall and Clements¹ say "relationship is the very essence of classification." New species should be described only as the result of experimental work which should seek "to determine the relationship by descent of the species and variads already in existence." The net results of this type of work should tend to reduce the number of species and, it is hoped, make an end of species splitting. It is possible that, "for North America," the great majority of "real species" had been described by the close of Gray's work; but to all such should be given this rating as a result of ecologic, analytic and synthetic studies and not because of the authority of Gray and his co-workers.

¹ The phylogenetic method in taxonomy. Hall, H. M., and Clements, F. E., Carnegie Institute of Washington, Publication 326.

II. SOME NATURAL VIOLET HYBRIDS OF NORTH AMERICA

By Ezra Brainerd

Some preliminary statement should be made regarding the investigations that lead to the formation of this list of 82 violet hybrids. writer's study of North American violets began in 1902; in this and the year following some 2,000 to 3,000 plants were collected from over 200 stations in Western Vermont and Western Massachusetts, an account being published in Rhodora. The importance of the cleistogamous flowers in distinguishing species of the acaulescent violets was emphasized and a synopsis of 10 New England species was presented based upon these apetalous flowers. At the close of the paper certain facts were alluded to as indicating the occurrence of hybrids. another season's study of the problem, I published² a detailed account of eight hybrids between five species of Viola from Western Vermont. The correctness of this conclusion has since been fully verified. interesting incident may be cited. In June, 1904, I had received from Watson of Charlottetown, P. E. I., three specimens of what seemed to be V. fimbriatula \times septentrionalis. But I was troubled by the fact that V. fimbriatula had never been reported from that region, nor from the Province of Quebec, Northern New Brunswick or Northern Maine. At my request, Watson kindly revisited the station for his hybrid and succeeded in finding there excellent specimens of V. fimbriatula. We are taught in inductive logic that one of the best possible verifications of an hypothesis is its ability to anticipate the discovery of facts not before observed.

I would allude briefly to my labors during the subsequent 17 years, in which I revised the specific names of the genus, examined specimens in all the large herbaria of the United States, collected specimens from every State in the Union but two and cultivated in my home garden thousands of plants. Meanwhile I studied the literature of the subject: Mendel's epoch-making experiments with peas (1866); Focke's Pflanzen Mischlinge (Berlin, 1881); and Bateson's Principles of Heredity (1909). Many of these authorities will be referred to in the course of this bulletin.

If we omit all hybrids in which either parent is only a variety, the number in our list would be reduced from 89 to 82 and it will be found

¹ Rhod. 6: 8-17, pl. 50, Jan., 1904. ² Rhod. 6: 213-222, pl. 58, Nov., 1904.

that only 30 species occur in the parentage of these 82 hybrids. A formula, deduced in Rhodora 6:214, tells us how to compute, when n is the number of species that hybridize, the number of possible combinations, N; viz.: $N = \frac{1}{2}n$ (n-1); or, in the case before us where n=30, $N=15\times 29=435$. Now we may well inquire, why is it that we here find only 82 hybrids and not the theoretically possible 435? There are two reasons: first, because the two parent species do not cohabitate, or grow so near together that the pollen of the one can be brought by wind or insects to the stigma of the other, and, secondly, because the botanist has not had the good fortune to make a timely visit to the hybrid's station. Our rare violet hybrids show that distantly related species may unite sexually, if there is only a favorable conjunction of time and place. Take for example V. Brittoniana \times lanceolata Forbes¹, an absolutely sterile hybrid that can be propagated only by division and that has been found only once.

We may conclude that any list of hybrid violets, like the one here presented, is more or less incomplete, though it may be the record of many years of careful observation and culture.

The 30 species that are as yet known to hybridize among the 75 recognized in North Amèrica are as follows:

		TIMES	of					
		OCCURE	NCE	;	TIMES	S		TIMES
$V_{\cdot \cdot}$	adunca	1	V.	latiuscula	3	V.	rostrata	2
V.	affinis	12	V.	Lovelliana	2	V.	sagittata	11
V.	Brittoniana	9	V.	missouriensis	1	<i>V</i> .	septentrionalis	4
V.	conspersa	2	V.	nephrophylla	5	V.	septemloba	1
V.	cucullata	12	V.	pallens	2	V.	sororia	15
V.	emarginata	9	V.	palmata	8	V.	Stoneana	4
V.	fimbriatula	12	V.	papilionacea	14	V.	striata	1
V.	hirsutula	7	V.	pedatifida	4	V.	triloba	11
V.	Langloisii	1	V	primulifolia	4	V.	viarum	1
V.	lanceolata	3	V.	rosacea	2	V.	vittata	1
		68			45			51

If we add the number of times the 30 species in this list occurs, it will be found to be 164, or twice the number of hybrids. Two species are cited in naming each hybrid; this requires the citing of specific names 164 times in a list of 82 hybrids.

¹ Rhod, 11: 14-5. Jan., 1909.

LIST OF THE 82 VIOLET HYBRIDS DISCUSSED IN THIS BULLETIN

	Name	STATIONS	SHEETS IN HB. E. B.	WHERE PUBLISHED
1.	V.~adunea imes conspersa.	Proctor, Vt. Little Notch, Bristol Vt.	5	Ined.
		Ex horto 1911, 1912. Ottawa, Ont., 1904.		
2.	V.~a finis $ imes Brittoniana.$	Bradley Ave., Staten Is., N. Y. Ex horto 1911.	2	Dowell, Bul. Torr. Cl. 37: 169, pl. 2, April, 1910.
3.	imes cucullata.	Middlebury, Vt. Eastern Conn. Ex horto from W. J. Vreeland.	4	Rhod. 8: 49. Distrib. 1910, No. 7.
4.	imes emarginata.	Englewood, N. J. Ex horto 1908, 1910.	2	Ined.
5.	imes fimbriatula.	Staten Island, N. Y. New Jersey. Pennsylvania. Ex horto.	15	Dowell, Bul. Torr. Cl. 37: 170, pl. 12.
6.	imes hirsutula.	Glen Alpine, D. C., 1908. Kenilworth, N. J., 1910.	7	Rhod. 8: 56. Rhod. 8: 119.
7.	imes nephrophylla.	Providence Is., South Hero, Vt., 1905, 1907, 1910. Ex horto 1906.	. 5	Rhod. 8: 50. Distrib. 1910, Nos. 8 and 9.
8.	imes palmata.	Penfield, N. Y., 1910. Ex horto 1911, 1912.	1	Torr. Bul. 37: 171, pl. 13, April, 1910.
9.	imes papilionacea	Woodridge, D. C. Medford and Plainfield, N. J. Tinicum, Pa.	15	Rhod. 8: 119.
10.	imes sagittata.	Patuxent, Md. Tinicum, Pa. Staten Is., N. Y. Milltown, N. J.	17	Rhod. 8: 55. Amer. Naturalist 44: 235. Distrib. 1910, Nos. 10 and 11.
11.	imes septentrionalis.	Knight's Is., North Hero, Vt. Middlebury, Vt.	5	Rhod. 6: 219.
12.	imes sororia.	Diadem Is., North Hero, Vt. Middlebury, Vt. Canandaigua, N. Y. New York Bot. Gar- den, from Quebec.	7	Rhod. 6: 221.

13.		Name	Stations	SHEETS IN HB. E. B.	WHERE PUBLISHED
Septemloba." N. Y. Fairfield and Stratford, Conn. Milton and Springdale, N. J. Science N. Science N. Steine N. Store of N. Y. Steine N. Steine N	.3.			7	Distrib. 1910, Nos. 18, 19 and 20.
Rhod. 8: 52		"septemloba."	N. Y. Fairfield and Stratford, Conn. Milton and	34	Torr. Cl. 32: 255, t. 17. Science N. S. 15: 940.
N. Y. Staten Is., N. Y. Fairfield, Conn. Staten Is., N. Y. Fairfield, Conn. Staten Is., N. Y. Distrib. 1910 Nos. 21 and 22. Dowell, Bul Torr. Cl. 37: 172.	15.	imes $emarginata.$	Hyattsville, Md.	1	Brainerd, Rhod. 8: 53 House, Rhod 8: 120, t. 71
ows, Dedham, Mass. 11, 14. 18.	16.	imes fimbriatula.	N. Y. Staten Is., N. Y.	, 12	Rhod. 8: 51 t. 67. Distrib. 1910 Nos. 21 and 22. Dowell, Bul Torr. Cl.
Hempstead, N. Y. Hempstead, N. Y. Torr. Cl. 37 173, t. 14. Distrib. 1916 No. 23. **No. Y.** Dayton, N. J. Stratford, Conn. Dedham, Mass. 19. ***x sagittata.** Riverdale, Md. Staten Is., N. Y. Long Is., N. Y. Long Is., N. Y. **Torr. Cl. 37 173, t. 14. Distrib. 1916 No. 23. **Rhod. 8: 59 Pl. 69. **Phouse, Rhod. 8: 51 House, Rhod. 8: 120. 20. **x sororia.** **X sororia.** **Torr. Cl. 37 173, t. 14. Distrib. 1916 No. 23. **Photo. 8: 59 Whose, Rhod. 8: 59 Where calle "Y. palm. **ta × setemloba."* 22. V conspersa × rostrata. **Plainfield, N. J. **Distrib. 191	17.	imes lanccolata.		_	Forbes, Rhod 11, 14.
N. Y. pl. 69. Dayton, N. J. Stratford, Conn. Dedham, Mass. 19.	18.	imes papilionacea.		8	Dowell, Bul Torr. Cl. 37: 173, t. 14. Distrib. 1910 No. 23.
Staten Is., N. Y. Long Is., N. Y. Long Is., N. Y. Rhod. 8: 5: House, Rhod. 8: 120. 20. × sororia. Fairfield, Conn. 21. × triloba. Milltown, N. J. Stratford, Conn. Stratford, Conn. 22. V conspersa × rostrata. Plainfield, N. J. Staten Is., N. Y. House, Rhod. 8: 5: where called "V. palmeta × settemloba."		imes pectinata. .	N. Y. Dayton, N. J. Stratford, Conn.	., 13	
21. × triloba. Milltown, N. J. 5 Rhod. 8: 5 where calle "V. palmeta × settemloba." 22. V conspersa × rostrata. Plainfield, N. J. 5 Distrib. 191	19.	imes sagittata.	Staten Is., N. Y.	2	Rhod. 8: 51 House, Rhod
Stratford, Conn. where calle "V. palmeta × settemloba." 22. V conspersa × rostrata. Plainfield, N. J. 5 Distrib. 191	20.	\times sororia.	Fairfield, Conn.	1	
ZZ V COURSECTOR X 1000 Com.	21.	imes triloba.		5	Rhod. 8: 55 where calle "V. palmo ta × sep temloba."
	22.	$V.\ conspersa imes rostrata.$		5	

	Name	Stations	SHEETS IN HB, E, B.	
23.	$V.\ cucullata imes fimbriatula.$	Newfane, Salisbury and Middlebury, Vo Jaffrey, N. H. New York. Connecticut. New Jersey.	28	Distrib. 1910, Nos. 34, 35, 36 and 37. Pollard, Bul. Torr. Cl.
		North Carolina.		24: 404, t. 314.
24.	imes nephrophylla.	Manchester, Vt.	1	011.
25.	\times palmata.	East Lyme, Conn.	1	
26.	imes $papilionacea.$	Northampton, Mass. Plainfield, N. J. North Tacoma, D. C. East Lyme and Southington, Conn. Yonkers, N. Y.	8	Rhod. 8: 56.
	× pectinata.¹	Woodmere, Long Is., N. Y.	1	
27.	imes primulifolia.	Woodmere and Rosedale, N. Y.	2	Rhod. 11: 115.
28.	imes $sagittata.$	Tinicum, Pa. Montclair, N. J.	7	Rhod. 8: 52. Distrib. 1910, No. 38.
29.	imes septentrionalis.	Silver Lake, Leicester Vt. Charlottetown, Prince Edward Island		Rhod. 6: 220. Distrib. 1910, Nos. 39 and 40.
30.	imes sororia.	Widely distributed from Vermont to Wisconsin and south to Virginia.	18	Rhod. 6: 222. Distrib. 1910, Nos. 41 and 42.
31.	imes triloba.	Lexington, Mass. East Lyme, Conn. Rochester, N. Y.	8	Rhod. 8: 56 as amended. Rhod. 11: 115.
32.	imes viarum.	Spontaneous in garden in 1912.	2	
33.	$V.\ emarginata imes fimbriatula.$	Washington, D. C. New Brunswick, N. J Philadelphia, Pa.	8	Rhod. 8: 57.
34.	imes Lovelliana.	Muskogee, Okla.	2	
	× palmata.²	Eutaw Springs, S. C.	1	
35.	imes papilionacea.	Brookland, D. C. Ivy Hill Cemetery, Philadelphia, Pa. Milltown, N. J.	4	

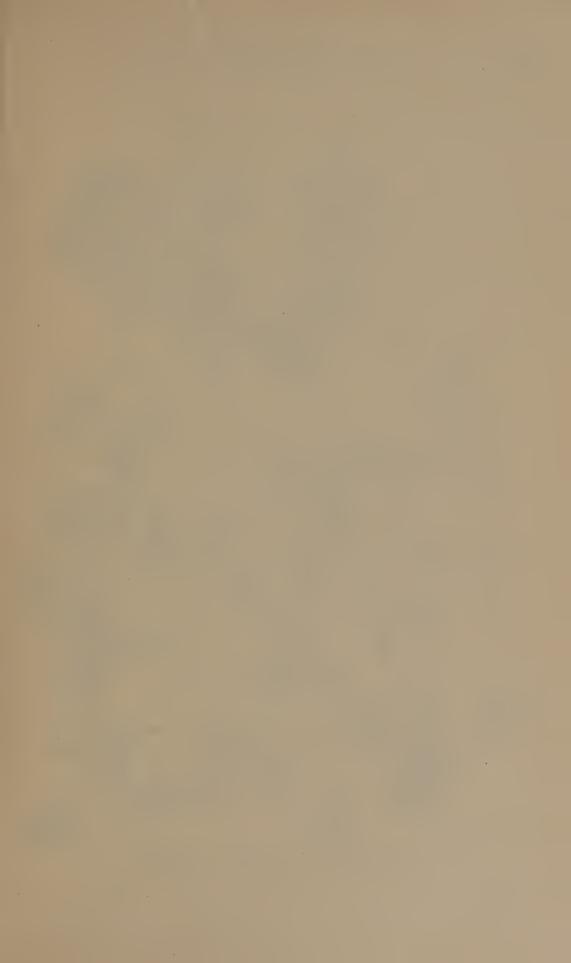
¹ See Vt. Sta. Bul. 224, pp. 69 and 123, ² Discarded for lack of sufficient evidence.

× sagittata. × septemloba × sororia. × Stoneana. × triloba.¹ × triloba.² var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³ briatula × hirsutula.	Brookland, D. C. Chester Co., Pa. Milltown, N. J. Gilmerton, Norfolk Co., Va. Carthage, Mo. Ivy Hill Cemetery, Philadelphia, Pa. Ex horto 1905, 1907. Tryon, N. C. Westville, Okla. Mena, Ark. Brookland, D. C. North Tacoma, D. C. Ex horto 1905, 1906, 1907, 1910.	1 1 1 4 1 5	3-4, fig. 1.
× sororia. × Stoneana. × triloba.¹ × triloba.² var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	Co., Va. Carthage, Mo. Ivy Hill Cemetery, Philadelphia, Pa. Ex horto 1905, 1907. Tryon, N. C. Westville, Okla. Mena, Ark. Brookland, D. C. North Tacoma, D. C. Ex horto 1905, 1906, 1907, 1910.	1 1 1 4 1 5	Torreya 14: 3-4, fig. 1.
× stoneana. × triloba.¹ × triloba.² var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	Ivy Hill Cemetery, Philadelphia, Pa. Ex horto 1905, 1907. Tryon, N. C. Westville, Okla. Mena, Ark. Brookland, D. C. North Tacoma, D. C. Ex horto 1905, 1906, 1907, 1910.	1 1 4 1 1 5	
× triloba.¹ × triloba.² var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	Philadelphia, Pa. Ex horto 1905, 1907. Tryon, N. C. Westville, Okla. Mena, Ark. Brookland, D. C. North Tacoma, D. C. Brookland, D. C. Ex horto 1905, 1906, 1907, 1910.	1 4 1 5	
× triloba.² var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	Westville, Okla. Mena, Ark. Brookland, D. C. North Tacoma, D. C. Brookland, D. C. Ex horto 1905, 1906, 1907, 1910.	1 1 5	
var. dilatata. arginata var. acutiloba³ × fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	Mena, Ark. Brookland, D. C. North Tacoma, D. C. Brookland, D. C. Ex horto 1905, 1906, 1907, 1910.	1 1 5	
× fimbriatula. var. acutiloba³ × sagittata. arginata lobed form × papilionacea.³	North Tacoma, D. C. Brookland, D. C. Ex horto 1905, 1906, 1907, 1910.	1	
× sagittata. arginata lobed form × papilionacea.	Brookland, D. C. Ex horto 1905, 1906, 1907, 1910.	5	
× papilionacea.3	Ex horto 1905, 1906, 1907, 1910.		
$briatula \times hirsutula.$	Hoch autorilla Ctatas Ta		
	Egbertville, Staten Is N. Y.	s., 0	Bul. Torr. Cl 37: 175, pl 15, 1910.
imes latiuscula.	Ft. Ethan Allen, Essex, Vt.	10	
× palmata.	Rochester, N. Y. Mt. Tryon, N. C. East Lyme, Conn. Spring Valley, N. Y.	10	Rhod. 15: 114 1910.
imes $papilionacea.$	Connecticut. New Jersey. New York. Pennsylvania. District of Columbia	. 22	Rhod. 6: 218 Rhod. 8: 54.
imes sagittata.	Massachusetts. Connecticut. New Jersey.	2 8	Rhod. 8: 57 pl. 68.
imes septentrionalis.	Maine. Middlebury, Vt. New Hampshire. Massachusetts. Prince Edward Island	20 d	Rhod. 6: 215 pl. 58.
	imes sagittata. $ imes$ septentrionalis.	New Jersey. New York. Pennsylvania. District of Columbia	New Jersey. New York. Pennsylvania. District of Columbia. × sagittata. Massachusetts. Connecticut. New Jersey. × septentrionalis. Maine. Middlebury, Vt. New Hampshire. Massachusetts. Prince Edward Island

	Name	STATIONS	SHEETS IN HB. E. B.	
46.	imes sororia.	Middlebury, Vt. Hempstead, N. Y.	4	Rhod, 6: 218 Distrib. 1910 Nos. 58 and 59.
47.	imes triloba.	Lexington, Mass. New Hampshire. Connecticut.	9	Rhod. 8: 53 pl. 70, for palmata read triloba.
48.	$V.\ hirsutula imes palmata.$	Plainfield, N. J.	4	Torr. Bul. 39:
49.	imes papilionacea.	Philadelphia, Pa. Ohio. North Carolina. Connecticut. New Jersey. District of Columbia.		Rhod. 9: 211. Science, N. S. 25: 941. Distrib. 1910, No. 66.
	imes sagittata.	Kenilworth, N. J. Ex horto 1911.	1	
50.	imes sororia.	New Jersey. Rockville, D. C. Tryon and Biltmore, N. C.	7	Torr. Bul. 37: 176, pl. 16.
51.	imes $Stoneana.$	Hyattsville, Md. Philadelphia, Pa. Brookland, D. C.	10	Torr. Bul. 39: 96. Rhod. 8: 121, pl. 12.
52.	imes triloba,	New Jersey. District of Columbia Virginia. North Carolina. Morristown, Tenn.		Rhod. 8: 56, as "V. pal- mata × villosa." Torr. Bul. 39:
53.	$V.\ lance olata imes pallens.$	Lake Harris. Newcomb, N. Y.	0	95. Bul. N. Y. St. Mus. 243, p. 26, 1921.
54.	imes primulifolia.	Several stations on Staten Island, N. Y	. 0	Torr. Bul. 37:
55.	$V.\ Langloisii imes rosacea.$	Crowley, La. Ex horto 1910.	1	176, pl. 17.
56.	$V.\ latius cula imes sororia.$	Lake Dunmore, Salisbury and West Rutland, Vt. Williamstown, Mass.	4	
57.	imes triloba.	Salamanca, N. Y. Ex horto 1910, 1912.	16	Torr. Bul. 39:
5 8.	V. Lovelliana $ imes$ papilonacea.	Edgewood, Okla. Ex horto 1910.	3	

	Name	STATIONS	SHEETS IN HB. E. B.	WHERE Published
59.	$V.\ missouriensis imes sororia.$	Kansas. Missouri.	2	
60.	V.nephrophylla imes papilionacea.	Racine, Wis.	4	Distrib. 1910, Nos. 87 and 88.
61.	imes pedatifida.	Beulah, New Mex.	0	Torr. Bul. 40: 259.
62.	imes sororia.	Manchester, Vt.	2	
	$V.\ odorata imes$	Bronx Park, N. Y. Florida.	2	
63.	$V.\ pallens imes primulifolia.$	Staten Is., N. Y. Seabrook, N. J.	4	Torr. Bul. 37: 177, pl. 18.
64.	$V.\ palmata imes papilionacea.$	Tryon, N. C. Plainfield, N. J. From Miss Kittridge Miss Angell Miss Kaufman	6.	Torr. Bul. 39: 85, pls. 5 and 6.
65.	imes $sagittata.$	Staten Is. and Rosedale, N. Y. West Orange, N. J. Haddonfield, N. J.	3	Rhod. 15: 115, No. 6.
66.	\times sororia.	Hamilton, Co., Ohio.	1	
67.	imes triloba.	Maryland Heights, Md. East Lyme, Conn. Orange, N. J. ² Argus, Bucks Co., Pa	2 0	Torr. Bul. 39: 88, pl. 7, figs. 3-7. Distrib. 1910, No. 97.
68.	V.~papilionacea imes pedatifida.	Yorkville, Ill.	75	Torr. Bul. 40:
69.	$V.\ papilionacea\ imes\ sagittata.$	Stark Co., Ill. Glastonbury, Conn. New Brunswick, N. 3 Staten Is., N. Y. Tinicum, Pa.	Г.	249, pl. 15. Rhod. 8: 54. Distrib. 1910, No. 113.
70.	imes $sororia.$	Southeastern New York. Ohio. Wisconsin. Kansas. Missouri. Louisiana.	13	Torr. Bul. 37: 178. Distrib. 1910, No. 114.
71.	imes Stoneana.	Ivy Hill Cemetery, Philadelphia, Pa.	9	Torr. Bul. 39: 93.
	¹ Exotic. ² 25 miles north of Philadelphia.			

	Name	STATIONS J.	неетs и Нв. Е. В.	
72.	imes triloba.	Along the coast from East Lyme, Conn. to South Carolina.	35	Torr. Bul. 39: 90.
73.	$V.\ pedatifida imes sagittata.$	Peoria Co., Ill.	20	Torr. Bul. 40: 252, pl. 16.
74.	× sororia.	Galva, Ill. 21. Ex horto Middlebury 115. Miscellaneous 18.	154	Torr. Bul. 40: 253-259, pl. 17.
75.	$V.\ primulifolia imes vittata.$	Chickasaw, Mobile, Ala.	7	
76.	V.rosacea imes sagittata.	Crowley, La. Ex horto 1910, 1911.	3	
77.	$V.\ rostrata \times striata.$	Cincinnati, O.	2	
78.	$V.\ sagittata imes sororia.$	Milwaukee, Wis. Ex horto 1910, 1907.	4	Distrib. 1910, Nos. 142 and 143.
79.	imes triloba.	New Brunswick, N. J. Ex horto 1906.	6	Rhod. 8: 54 [where for palmata read tri- loba]. Rhod. 15: 115.
80.	$V.\ septentrionalis imes sororia.$	Middlebury, Vt., 3 stations. Arlington, Vt.	6	Rhod. 6: 221. Distrib. 1910, No. 157.
81.	$V.\ sororia imes triloba.$	Orwell, Vt. Connecticut. Long Island, N. Y. New Jersey. Biltmore and Tryon, N. C.	12	Torr. Bul. 39: 92.
82.	V.Stoneana imes triloba.	Ivy Hill Cemetery, Philadelphia, Pa.	14 5	 Forr. Bul. 39: 93. Am. Naturalist 44: 231.





Hybrid No. 1—Viola adunca imes conspersa

1. Viola adunca \times conspersa Brainerd.

Leaf-blades broad and blunt as in V. conspersa; stipules sparsely serrulate as in V. adunca, not coarsely serrate as in V. conspersa; cleistogamous flowers in autumn abundant from axils of upper leaves as in V. conspersa, mostly sterile; some plants puberulent as in typical V. adunca, others quite glabrous as in V. conspersa.

Specimens in my herbarium are from these stations: (1) Proctor, Vt., Eggleston, No. 3279, September 1, 1903, (2) shady slopes in Little Notch, Bristol, Vt., June 11, 1907; (3) near Rideau Hall, Ottawa, Ont., September 3, 1904—passing with the late Dr. James Fletcher as *V. subvestita* Greene, Erythea 5: 39, 1897, a synonym of *V. adunca*.



Viola affinis X Brittoniana Dowell, Bul. Torr. Cl. 37: 169-170, pl. 2. April, 1910.

Glabrous, excepting a slight puberulence on the upper surface and margin of leaf. Blades of leaf deltoid, with a broad shallow sinus 2½-7 cm. long and the later leaves as broad, on petioles two or three times as long; margin cut about midway to the mid-vein into falcate lobes, the basal lobes broad and incised, the median lobe terminating the blade with a blunt apex. Scapes of blue flowers about equaling the petioles; auricles of calyx, ciliolate, short and oppressed or long and spreading; cleistogamous capsules green or purplish, finely puberulent or glabrate, about 1 cm. long, on ascending or erect slender peduncles about half as long as the petioles; seeds buff.

In their vernal stage these plants resemble V. Brittoniana, but the leaves are less deeply cut. The long-auricled calyx of the cleistogamous flowers shows also the relationship to this species. On the other hand the purple-mottled and puberulent capsules are unmistakable evidence of the relationship to V. affinis.

Live plants of this hybrid were sent by Dowell, July 1, 1910, from Staten Island, N. Y., and were grown in my garden at Middlebury, Vt., and observed till June 25, 1911. The foliage was quite intermediate between that of the parent species; the capsules were hairy as in a form of *V. affinis*, and most of them contained aborted ovules.

3. Viola affinis × cucullata Brainerd, Rhod. 8: 49. March, 1906.

Differing from V. affinis in having larger leaves, a dark-blue ring around the center of the open corolla, long slender apetalous flowers, and in having long-auricled sepals; in these four respects approaching V. cucullata; differing from V. cucullata in having subacuminate leaves, purplish petals, a somewhat bearded spur-petal, and in having cleistogamous capsules dotted with brown; in these four aspects approaching V. affinis. It has all the characters common to the two parents—except fertility.

A specimen found in an alder thicket along the river in the north-west part of Middlebury, Vt., was cultivated from 1903 to 1906, and spontaneously reproduced four seedlings quite like itself. A similar plant received from Vreeland (Montcalm, N. J.) in July, 1907, was grown till May, 1910. See No. 7 of my Distribution in 1910 of Eastern North American Violets.



Hybrid No. 4—Viola affinis × emarginata

4. Viola affinis × emarginata Brainerd.

Plants in contour, size and dentation of leaf and in color of capsule quite intermediate between the two parent species, at the same time possessing all their common characters—color of flowers and of seeds and lack of pubescence.

In October, 1906, Miss A. M. Ryan sent living plants from Englewood, N. J., which with their offspring were grown for four years, giving abundant evidence of their hybrid origin.



5. Viola affinis × fimbriatula Dowell, Bul. Torr. Cl. 37: 170-171, pl. 12. April, 1910.

Young plants pubescent, older plants much less pubescent. Vernal leaf-blades oblong-ovate to broadly ovate, obtuse or acutish, subcordate or truncate, crenate, or irregularly toothed toward the base, densely ciliolate, 2.5-4 cm. long, 1.5-3 cm. wide, on slender petioles two to three times as long; aestival leaves deltoid to ovate, with the apex more acute, 3-9 cm. long, 2.5-6 cm. wide. Blue flowers overtopping the leaves, their calyx lobes short and blunt, ciliolate, with short appressed ciliolate auricles; cleistogamous flowers sagittate, with longer and more spreading ciliolate auricles, on erect or ascending peduncles; capsules green or mottled with purple, puberulent or glabrous, 6-11 mm. long, in some plants entirely sterile; seeds buff to brown.

This hybrid is common on Staten Island, N. Y., where Dowell collected it at five stations. It is admirably represented in his plate.

Several living plants from Staten Island were received in October, 1906, from Miss Ryan, and later from Dowell, both sets unnamed. These plants and their seedlings were cultivated for several years in my home garden. In October, 1906, Miss Ryan sent it also from Englewood, N. J., and in May, 1910, I received a plant from F. N. Pennell, collected in Wawa, Pa., about 20 miles west of Philadelphia.

The study of this hybrid has been perplexing because of the frequent confluence of typical V. sagittata with V. fimbriatula.

¹ See Rhodora 8: 57, March, 1906.



Hybrid No. 6—Viola affinis \times hirsutula

6. Viola affinis × hirsutula Dowell Bul. Torr. Cl. 37: 171. April, 1910.

V. affinis × villosa Brainerd, Rhodora 8: 56. March, 1906.

Rootstock fleshy, erect. Plant rather low, glabrous except the upper surface and margin of leaf, which has the characteristic pubescence of *V. hirsutula*. Blades of leaves broadly ovate to deltoid-ovate, acutish, but with a blunt tip, deeply cordate to nearly truncate at the base, 4-9 cm. long, 3.5-5 wide, on slender petioles about twice their length, margin crenate-serrate with low teeth. Ripe but rather infertile capsule glabrous, about 7 mm. long.

"Only one little plant of this was found on Staten Island, in the woods west of Egbertville, August 23, 1909 (6005). This was in a little patch of *V. hirsutula* with plenty of *V. affinis* growing near.

"The change in the name of the hybrid is due to the fact that V. hirsutula Brainerd takes the place of V. villosa of authors, not Walt."

The range of the hybrid as indicated in the Brainerd Herbarium is from Washington, D. C., and vicinity to Plainfield, N. J. Three living plants from the vicinity of Cincinnati, Ohio., sent by E. Lucy Braun, 1913, seem to be this hybrid.

¹ Rhodora 9: 98, June, 1907.



7. Viola affinis × nephrophylla Brainerd, Rhod. 8: 50. March, 1906.

Leaf-blade broadly ovate as in V. nephrophylla, not narrowly ovate as in V. affinis, capsules spotted with purple as in V. affinis, not green as in V. nephrophylla; seeds olive-brown as in V. nephrophylla, not buff as in V. affinis.

This hybrid was first found July 4, 1905, growing with numerous plants of V. nephrophylla on Providence Island, in Lake Champlain, southwest of the town of South Hero, Vt. Its sterility and unfamiliar aspect indicated a hybrid and suggested V. affinis as the other parent. On July 22, 1905, on revisiting the island, I found many other specimens of the hybrid and transferred plants to my garden in Middlebury, from which petaliferous flowers were obtained the following year. From these plants or their seedlings numerous herbarium specimens were made from 1906 to 1910. In June, 1907, live plants of this hybrid were sent by Dr. Ogden of Milwaukee, Wis., from "a boggy meadow near a stream from a cold spring." These were grown for at least three years.

¹ See No. 9 of my distribution, 1910. ² See No. 8 of my distribution, 1910.



Hybrid No. 8—Viola affinis × palmata

8. Viola affinis × palmata Dowell, Bul. Torr. Cl. 37: 171, pl. 13. April, 1910.

Plant with scattered pubescence, intermediate in general appearance between the woodland form of *V. affinis* and *V. palmata*. Rootstock rather slender. Blades of leaves broadly triangular-ovate, 6-9 cm. long, 7-10 cm. wide in fully developed leaves, on slender petioles two or three times as long; apex obtuse, base with a broad sinus; margin ciliolate, irregularly toothed or shallowly lobed. Cleistogamous capsules purple-mottled, slightly puberulent, about 7 mm. long, on short ascending peduncles; calyx-lobes purplish, short, blunt, with short ciliolate auricles; seeds brown.

A small colony, Dowell (5615), was found in the woods west of Egbertville, Staten Island, N. Y. Only one other station is known—Penfield, N. Y. Slavin, of the Park Department, Rochester, N. Y., transferred it to his grounds, May 10, 1910, and sent the writer plants October 27, 1910, which were grown for two years. The hybridity of the plant was indicated by the sterility of its capsules, and its parentage is fairly well revealed by the blending in foliage, flower and fruit of the characters of *V. affinis* and *V. palmata*.



Hybrid No. 9—Viola affinis × papilionacea

9. Viola affinis × papilionacea House, Rhod. 8: 119. July, 1906.

Blades of leaf broader and plant much larger than in normal V. affinis; flowers intermediate between those of parent species; capsules distinctly pubescent as in a local form of V. affinis, its ovules mostly aborted.

This hybrid was discovered by House at Woodridge, D. C. On a moist wooded hillside grew a large colony of V. affinis and at the base of the hill in a meadow V. papilionacea was abundant. On May 3. 1906, House noticed an abundance of what seemed a darker and broader-leafed form of V. affinis growing lower down on the hillside than the typical V. affinis. The intermediate character of its leaves and flowers suggested its hybrid origin, which when fruit was secured, June 15, 1906, was placed beyond further doubt, the distinctly pubescent capsules containing aborted ovules, and the plant as a whole being much larger than typical V. affinis. Specimens of both these dates—"cotypes"—are in the Brainerd herbarium.

In September, 1905, living plants were received from Medford, N. J., collected by Witmer Stone, from which herbarium specimens in flower were made May 14, and in fruit August 26, 1906. A third station was found at Plainfield, N. J., and a fourth at Tinicum, Pa., September, 1906. From plants received from these stations and grown in my garden in Middlebury, seedlings were raised for several years.

Viola filicetorum Greene and its var. parthenica¹ from District of Columbia, April and May, 1906, are apparently the hybrid here discussed.

¹ Leaflets, 1: 215, June 5, 1906.



Hybrid No. 10a-Viola affinis × sagittata and parent species

10. Viola affinis × sagittata Brainerd, Rhod. 8:55. March, 1906.

Leaves narrowly deltoid, the upper half minutely and distantly serrate, the basal lobes round and coarsely toothed, forming a broad sinus; cleistogamous flowers and fruit intermediate.

This hybrid was first recognized in specimens collected at Patuxent, Md., June 4, 1905, House, No. 972. With these was growing an aberrant form of V. affinis, bearing minutely pubescent capsules; but the hybrid had also this aberrant mark which thus proved its affinis parentage. Three months later (September 6, 1905), in company with Witmer Stone, I collected the hybrid at Tinicum, Pa., growing in an open bay with V. affinis; V. sagittata was found at no great distance. Plants of the Tinicum hybrid and from Staten Island, Dowell (4681) and their seedlings were grown during the five succeeding years. Other stations are Plainfield and Glastonbury, Conn.; also Milltown and Kenilworth, N. J.

An account of an experimental culture is added from American Naturalist 44: 235-236, April, 1916.

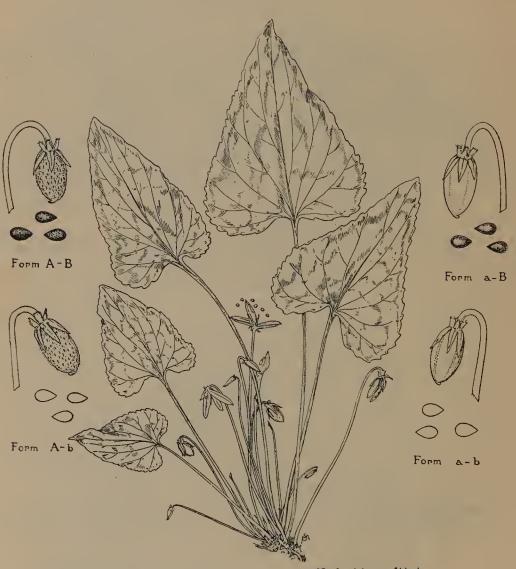
It frequently happens that a subhybrid form in *Viola* is so unlike either parent of the first-cross as to appear to be specifically distinct. Many such violet hybrids have in recent years been named and published as species: *V. Mulfordæ* Pollard, *V. notabilis* Bicknell, *V. cucullata* House and *V. aberrans* Greene are specific names that have been given to four now well known hybrids. It is surely hazardous in

¹ See Nos. 10 and 11 of my Distribution of Eastern North America Violets, and drawings of its segregating offspring.



our present knowledge of the genus to put forth as a species a newly discovered form of Viola, without studying it through at least one season of growth and through one generation of offspring. It may, indeed, transpire that the new form, though of hybrid origin, is distinct and stable; and if fairly wide-spread, it may be entitled to specific or varietal rank. The bar sinister in the escutcheon of its bastard ancestry may have been quite obliterated. We may be here witnessing the birth of a new species through hybridism. I present an instance that makes a close approach to these conditions.

In May, 1906, Mr. Stone sent me from Tinicum, Pa., a living violet plant that was quite fertile and appeared a good species. I could not make it out a hybrid, though perhaps predisposed at that time to place an anomalous form in this category. For further light I visited the station with Mr. Stone the following September; but the most careful search failed to reveal another specimen. It soon afterward occurred to me that it might be an offspring of V. affinis \times sagittata, a hybrid which I had found at the same place the year previous, and had transferred to the garden. The two plants, mother and supposed daughter, appeared much unlike, the former being quite infertile, and in most respects an excellent intermediate between the putative parents that grew near by. But careful examination showed that, though no one character of the supposed daughter was intermediate as in the mother, yet all were to be found in one or the other of the supposed grandparents. The leaves had the breadth and the rounded basal lobes of V. affinis,



Hybrid No. 10c—Segregates of Viola affinis imes sagittata

but the length and the attenuate apex of V. sagittata; the capsules were pubescent as in V. affinis, but green and large as in V. sagittata; furthermore, the peduncles were strictly erect as in V. sagittata, not ascending as in V. affinis; and also the seeds were brown as in V. sagittata, not buff as in V. affinis.

The next move was to raise offspring of the plant, to discover if some one of these characters was not impure—in other words, dominant and holding latent the opposed character. The 23 plants subsequently raised showed all the characters of the plant under investigation to be pure excepting two, the pubescence of the capsules and the dark-brown color of the seeds; for glabrous capsules and buff seeds appeared in some of the offspring. The ratio of the four Mendelian forms in the 23 plants was 12: 4: 4: 3, or 9: 3: 3: 2½, an unexpectedly close approximation to the theoretical ratio 9: 3: 3: 1.

From eleven of these plants another generation of 204 plants was raised. Among these in addition to the five possible hybrid forms, were obtained also the four possible stable forms. So that I now have fertile plants, free of all hybridity, of four sorts, viz., 18 with pubescent capsules and dark seeds, 9 with pubescent capsules and buff seeds. 18 with glabrous capsules and dark seeds, 44 with glabrous capsules and buff seeds.

Surely, what I have done in the garden, nature might do in the wild, thus evolving a distinct species with three varieties.



Hybrid No. 11-Viola affinis × septentrionalis

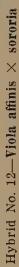
11. Viola affinis × septentrionalis Brainerd, Rhod. 6: 219-220. Nov., 1904.

Petioles and under surface of blades usually glabrous as in V. affinis, but sometimes pubescent as in V. septentrionalis; sepals somewhat ciliolate more so than in V. affinis, less so than in V. septentrionalis; seeds few, buff as in V. affinis; capsules numerous, but smaller than in either parent species, containing mostly aborted ovules.

This hybrid was first found on Knights Island in the northern part of Lake Champlain—a mile and a half southeast of North Hero "City," the shire town of Grand Isle County, Vt. For several years I had camped on this island and had thoroughly explored its botany, but had found only two species of "blue stemless violets," namely V. affinis and V. septentrionalis. On June 28, 1903, I was perplexed at finding several specimens of Viola that I could not satisfactorily place in either species. I was further troubled by failing to find plump full-grown capsules, although there were plenty of small seemingly immature ones. I visited the station the following year, July 24, 1904, when I found 33 seedlings closely clustered around the roots of the anomalous plant, none bearing more than one or two leaves. These seedlings I transplanted to my home garden. Many of them produced in September cleistogamous capsules, all lacking seeds, showing that the partial sterility of the mother hybrid was inherited by its offspring.

A second station for this hybrid was found near Middlebury, May 15, 1904, in an open maple grove. The ground was gay with the large violet flowers of *Viola septentrionalis*, and in the moister hollows of the ledges there was an almost equal profusion of *V. affinis*. Careful search revealed intermediate forms. One of these transferred to the garden produced in September more than 50 capsules, all showing the characteristic infertility of the hybrid.

I have never seen a specimen of this hybrid from any station outside of the Champlain Valley. This is explicable when we reflect that V. septentrionalis (literally the "northern violet") is not known to occur south of New England, and that V. affinis is apparently wanting in Eastern New England. The parents of a hybrid must needs be cohabitant.





12. Viola affinis × sororia Brainerd, Rhod. 6: 221-222. Nov., 1904.

Plants in size and outline of leaf-blades intermediate between the parent species; their petioles somewhat pubescent as in V. sororia, not glabrous as always in V. affinis; seeds in some plants dark-brown as in V. sororia, in other plants buff as in V. affinis.

Specimens of this hybrid in my herbarium are from four stations: First, a small island of four or five acres about $2\frac{1}{2}$ miles east of North Hero "City," the shire town of Grand Isle County, Vt. On the north end of the island is a large lagoon of stagnant water, made by the joining of two sand-bars driven northward by wave-action from the two sides of the island. In the moist leaf-mould on the borders of this pool grew luxuriant specimens of V. affinis, and a little farther back in drier and more shaded spots were colonies of V. sororia; and no other species of blue stemless violets were to be seen on the island. Not far from these two species I discovered (August 6, 1903) a colony of plants intermediate in foliage and pubescence, all the capsules of which seemed but half grown, although many of them contained ripe seed. Subsequent study of these specimens proved them to be a cross between the two associated species.

The second station was in the orchard of my home in Middlebury, where the hybrid and its parents were found to be abundant, and the evidence from intermediacy and infertility quite convincing. Ten small capsules, all that had matured on one plant, contained in the aggregate only 62 seeds.

The third station for this hybrid is Lake Leamy, Quebec. A plant collected here by Fletcher was grown in the Bronx Park garden, from which I obtained a specimen September 11, 1905.

The fourth station is Canandaigua, N. Y., whence live plants were sent me May 31, 1912 by Miss E. G. Webster.



Hybrid No. 13—Viola affinis \times triloba

13. Viola affinis × triloba Brainerd.

Plants quite diversiform in leaf outline:—some having uncut blades as in V. affinis, others markedly dissected as in V. triloba. In respect to pubescence most plants glabrous as in V. affinis, a few more or less hirtellous on the upper surface as in V. triloba.

The plant, from cultures of which this hybrid was studied in my garden in Middlebury, was sent by Miller (No. 12) from Plainfield, N. J., September, 1906. The original plant was multiplied by division of the rootstock and by raising several broods of its offspring during the three following years.

A TABULAR VIEW OF LEAF-FORMS IN SEVEN HERBARIUM SPECIMENS

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Sheet 3 Sept. 9, 1907 Sept. 16, 1908 Sheet 3 Sheet 4 Sheet 5 Sheet 6 Sheet 6 Sept. 16, 1909 Oct. 11, 1909 Sheet 6 Sept. 28, 1908 Sheet 6 Sheet 6 Sept. 28, 1908 Sheet 6 S
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I would place here specimens that I collected in Tryon, N. C., April 17, 1909, seven heterophyllous plants nearly or quite glabrous; also a sheet of seven plants collected by Deam (No. 6460) in white oak woods Clark County, Ind., May 25, 1910, in 38.5° north latitude.



Hybrid No. 14—Viola Brittoniana \times cucullata

14. Viola Brittoniana × cucullata House, Bul. Torr. Cl. 32: 255, pl. 17. May, 1905.

V. notabilis Bicknell, Torr. 4: 131, Sept., 1904.

V. cucullata × septemloba Brainerd, Rhod. 8: 52, March, 1906.

Glabrous, light-green, 1.5-2 dm. tall; mature leaves triangular or triangular-ovate in outline, shallowly cordate or nearly truncate, divided into 5-9 somewhat irregular lobes, the lobes cut one-half to two-thirds of the distance to the petiole, the margins irregularly crenate-dentate; petioles two to three times as long as the blades; cleistogamous flowers and capsules also similar to V. cucullata but the peduncles shorter.

Bicknell, the first to observe this new form of Viola in Woodmere, on the south shore of Long Island, N. Y., near Rockaway Beach, published it with a detailed description as V. notabilis. He states that it is often found growing with, or near, $Viola\ Brittoniana$, to which it is closely related but it is much larger in every way, of more tufted habit, the leaves much less divided, with broader, shorter, more obtuse lobes, the flowers deeper in color with broader petals, the sepals usually distinctly ciliolate. He says "V. $Mulforda^1$ is at once distinguished from V. notabilis by the pubescence of the former and its more oblong leaves, as well as by its smaller general size and smaller flowers on relatively shorter peduncles."

Stone was the first to discover the hybrid nature of the plant and to name correctly the two parent species. He collected it at Springdale, N. J., June 27, 1903, and the following October with some hesitancy wrote²: "Viola Brittoniana × Viola cucullata would, to my mind, produce just such a plant as this and at this spot they both occur intermingled."

From this Springdale colony I received living plants from Stone, May, 1907, which, with their offspring, were under cultivation for over three years. Specimens were distributed in 1910 as Nos. 18, 19 and 20 of my Violets of Eastern North America.

¹ V. Brittoniana × fimbriatula, hyb. No. 16. ² Proc. Acad. Phila., p. 680, 1903.

Living plants of this hybrid were sent me by Eggleston and House in June, 1904, from Milltown, N. J., and were grown with their off-spring for at least five years. Many reversionary forms were found in the seedlings of these plants, interesting recombinations of the opposed characters of the parent species in respect to outline of leaf-blades, varying from deeply dissected to uncut forms, and in color of seeds, varying from buff to brownish and dark-brown.

Other stations from which specimens came were Stratford and Fairfield, Conn., where, in fields bordering salt meadows, the hybrid was growing with both parents and completely sterile, but exhibiting great vegetative vigor, the clumps often a foot in diameter. In 1907 plants were sent by Dowell from Staten Island, N. Y.

I present with some emendation an extract from a paper read at the Boston (1906) meeting of the American Association for the Advancement of Science and published in *Science*, June 14, 1907.

THE BEHAVIOR OF THE SEEDLINGS OF CERTAIN VIOLET HYBRIDS

"During the summer of 1906 I raised plants from the seeds of twenty-five different hybrids of *Viola*, and also from the seeds of about twenty pure species. The behavior of these two classes of seedlings was surprisingly unlike; the offspring of the pure species resembled each other closely, but the offspring of the hybrids were often much unlike each other and unlike their immediate parents, reverting in some qualities to one parent of the hybrid and in other qualities to the other parent, and this in a great variety of ways.

"The species involved in these experimental cultures all belong to the group commonly known as 'blue stemless violets,' of which V. palmata. V. cucullata and V. sagittata are familiar examples. Of this group there are about twenty species in the northeasten United States, closely allied species,

that when growing together, freely interbreed.

"One of the corollaries of Mendel's law is that each pair of contrasting characters in a hybrid works out its effects, for the most part, independently of all other pairs. As in Newton's 'Law of the Coexistence of Motion,' the final result is but the summing up of the various component movements taken separately. It will be simpler for us, therefore, in describing the behavior of violet hybrids, to consider each pair of characters by itself, taking up, here,

the divergence that occurs in respect to leaf-outline.

"1. A striking illustration of diversity in leaf-form was seen in the off-spring of *Viola Brittoniana* × cucullata. This hybrid was published by Mr. Bicknell in September, 1904, as a species, *V. notabilis*. It has been found in five different stations, always growing with the reputed parents. In June, 1904, I received from New Jersey one of these plants that I have grown now for three seasons. From its cleistogamous capsules, which of necessity give pure cultures, I collected seeds in 1905 that furnished the following summer ten vigorous plants. These bore in August and September an abundance of cleistogamous flowers that matured seeds; several plants bore also in the autumn petaliferous flowers.

"The leaves of the parent species are very dissimilar, that of *V. cucullata* being broadly heart-shaped and pointed, that of *V. Brittoniana* primarily 3-parted, with the segments 2-4 lobed. The hybrids of these two species in all the five known stations exhibit a fair compromise in leaf-outline between the two quite unlike leaves of the parents, and closely resemble each other. They show about the same number of lobes as in *V. Brittoniana*, but the lobes are shorter and broader, the sinuses only half as deep. But in the offspring of this hybrid we have in addition to plants with this compromise leaf-form, plants with leaves but slightly lobed and showing the cordate base and acute apex of *V. cucullata*, and still other plants in which the leaf-outline is almost a complete reversion to *V. cucullata*. In the living plants that display, each, twelve or more leaves of these several patterns, the impression of dissimilarity is most striking."



Hybrid No. 15—Viola Brittoniana \times emarginata

15. Viola Brittoniana × emarginata House, nom. nov., Rhod. 8: 120, pl. 71. July, 1906.

V. emarginata × septemloba Brainerd, Rhod. 8:53. March, 1906.

"Aestival leaves simulating those of V. palmata, but quite glabrous; truncate at base or shallowly cordate; middle lobe often narrowly deltoid; autumnal and earliest vernal leaves but slightly incised; cleistogamous flowers on erect peduncles, producing green capsules 8-12 mm. long, quite infertile, the average number of seeds in 28 capsules being about one-fifth the normal number," [Brainerd in Rhod. 8: 53.1

This hybrid was a long time in securing due recognition. In 1897 Greene wrote¹: "My researches have demonstrated that V. emarginata * * * * very commonly presents a foliage as much cut palmately as V. palmata itself." Two accompanying plates drawn by Holm (Nos. 7 and 8) are unmistakably the above-named hybrid. A dozen live plants sent by Holm from Brookland, D. C., showed remarkable vigor under cultivation.

In December, 1903, Stone figured four leaves of plants from Tuckahoe, Cape May County, N. J.,2 collected August 25, 1901, that are doubtless of this hybrid and were growing with both parent species.

In my Rhodora paper of March, 1906, the specific name "V. septemloba" was incorrectly used instead of V. Brittoniana, a name not then recognized at Cambridge. I was grateful for the correction made by House in Rhodora, July, 1906, accompanied by his admirable plate 71.

¹ Pitt. 3: 255-256, Dec., 1897. ² Proc. Acad. Phila., p. 685, pl. 36, fig. 5.



Hybrid No. 16—Viola fimbriatula \times septemloba

- 16. Viola Brittoniana × fimbriatula Dowell, nom. nov., Bul. Torr. Cl. 37: 172. April, 1910.
- V. fimbriatula × septemloba Brainerd, Rhod. 8: 51, pl. 67. March, 1906.

"Vernal plants resembling V. Brittoniana; differing in having peduncles and petioles pubescent, calyx-lobes ciliolate, middle lobe of leaf longer. Aestival plants differing from V. Brittoniana in having larger leaves, with the middle lobe prominent, blades pubescent, on petioles about twice as long as blades. Cleistogamous capsules green, 12 mm. long, with some of the ovules aborted; seeds brown." [Dowell.]

This plant was first published by Pollard as V. Mulfordæ, based on specimens collected by Miss F. A. Mulford at Hempstead Plains, Long Island, N. Y., May 13, 1902. Through the kindness of Miss Mulford I received, September, 1904, 10 or 12 plants of her violet, which were under observation in the garden during the season of 1905. They had the usual vigorous growth of a hybrid and produced numerous cleistogamous flowers, most of which were quite sterile, turning yellow after a few weeks. In those that formed seed the average number produced was 45%. The intermediate character of the foliage is shown in plate 67, above cited, made in September from a plant in cultivation. Mixed with the living plants received in 1904 were five plants of V. Brittoniana and one of V. fimbriatula, showing that the three forms, the hybrid and its suspected parents, were growing near to each other. Later similar violet plants were found at other stations, from Fairfield, Conn., in 1906 by Dr. Eames, growing with V. Brittoniana and not far from V. fimbriatula;, and from Staten Island, N. Y., sent by Dowell in 1908, who obliged me by publishing the correct name of the hybrid given above.

¹ Proc. Biol. Soc., Wash., 15: 203, Oct. 1902.



Hybrid No. 17-Viola Brittoniana × lanceolata and parent species

17. Viola Brittoniana × lanceolata Forbes, Rhod. 11: 14-15. Jan., 1909.

Regarding this most remarkable of violet hybrids I quote an account in the original publication.

"Leaves with the color of those of V. lanceolata; much more lanceolate in outline, less deeply parted, and more rounded at base than those of V. Brittoniana; the leaves of the stolons entire, similar to but somewhat broader than those of V. lanceolata; petaliferous flowers differing from those of V. Brittoniana chiefly in their larger size; apetalous flowers numerous, on peduncles about the length of the petioles, withering early, always, infertile; stolons three or more inches long, vigorous, bearing leaves and apetalous flowers; pubescence and time of flowering like that of V. Brittoniana."

Only one plant of this violet hybrid has ever been found. In the fall of 1906, Forbes observed it on the Charles River meadows, Dedham, Mass., growing with V. lanceolata and not far from V. Brittoniana. Transferred to his violet bed for further study, it survived the winter and blossomed freely the following spring. The flowers were somewhat larger than those of V. Brittoniana but of the same blue color and general appearance.

During the summer and fall numerous cleistogamous flowers appeared, but all were completely sterile. In the spring of 1908 several small plants were made by division, blossomed profusely and in July produced leafy stolons more than three inches long, bearing apetalous flowers like those of *V. lanceolata*.

We present a plate of the original specimen of this hybrid and of the parent species in flower and in fruit.



Hybrid No. 18—Viola Brittoniana \times papilionacea

18. Viola Brittoniana × papilionacea Dowell, Bul. Torr. Cl. 37: 173, pl. 14. April, 1910.

"Slightly pubescent on the upper surface and margin of leaves, otherwise glabrous, 1.5-3 dm. tall. Rootstock fleshy, short, erect or ascending. Vernal leaves purplish beneath, ovate, obtuse, crenate or lobed; aestival leaves ovate to broadly triangular-ovate, irregularly toothed, or cut into falcate toothed or incised lobes, apex acute or obtuse, base cordate to truncate, blades 4-8 cm. long, 3-11 cm. wide, on petioles about three times as long. Petaliferous flowers large, the beard on lateral petals not strongly knobbed, peduncles equaling or shorter than the petioles; cleistogamous flowers sagittate, on short decumbent or ascending peduncles; capsules greenish, mottled with purple, about 1 cm. long; seeds as in V. Brittoniana.

"In its vernal stages it resembles the corresponding crosses with *V. affinis* and *V. cucullata*, but later its cleistogenes serve to determine its relationship without doubt. A large vigorous clump was found in a meadow on the east side of Bradley Avenue, Staten Island, May 23, 1909; (5658), transplanted, and specimens collected in July and August."

At the same date Dowell sent me a plant which was cultivated with its seedlings for over two years. From sowing 662 were obtained No. 23 in my 1910 Distribution of Eastern North American Violets.

In May, 1911, this hybrid was received from Miss Mulford. From its seeds, sowing 972, were obtained four forms of reversionary plants, differing widely in form of leaf and in color of seeds; specimens of which, made September 28, 1912, are now in my herbarium.



Hybrid No. 19—Viola Brittoniana imes sagittata and leaves of parent species

- 19. Viola Brittoniana × sagittata, House, nom. nov., Rhod. 8: 120. July, 1906.
- V. sagittata × scptemloba Brainerd, Rhod. 8: 51, pl. 66. March, 1906.

Blades of leaf strikingly intermediate between those of the parent species: at the base deeply dissected as in V. Brittoniana, not hastately lobed as in V. sagittata; the upper division lanceolate as in V. sagittata, or somewhat 3-lobed as in V. Brittoniana.

The type of this hybrid was collected by House at Riverdale, Md., May 1, and June 8, 1905, growing with the parent species and was at once recognized by him as a hybrid. Figures c and d of plate 66 are copied from plants collected at the same time and place as the hybrid a and b.

In the National Herbarium there is a specimen with leaves quite like those of the Riverdale plant, collected by Wm. T. Davis, New Dorp, Staten Island, N. Y., July 29, 1889, and labeled "V. sagittata." I have a specimen, also from Staten Island, collected at Midland Beach, May 22, 1910, by Dowell, and one from Hempstead Plains, Long Island, N. Y., collected by W. C. Ferguson, May 24, 1920.

The specimens furnish a good illustration of a blend hybrid, all of them presenting characters quite intermediate between those of the parents.



Hybrid No. 20—Viola Brittoniana × sororia

Viola Brittoniana × sororia Dowell, Proc. Staten Island Asso.,3: 161. May, 1911.

"Plant pubescent with fine spreading hairs. Rootstock thick, ascending. Blades of vernal leaves 2-4 cm. long, 1.5-3 cm. wide, ovate, mostly acute, cut-toothed or cleft, with a prominent middle lobe constituting the main part of the blade, on petioles two to four times as long; later leaves larger and wider in proportion to their length, some of the blades much wider than long and uncut; blue flowers on scapes as long as the petioles; cleistogenes prostrate or ascending, the scapes 6-15 cm. long; sepals lanceolate, two-thirds to one-half as long as the capsules, glabrous except on the prominent ciliolate auricles; capsules 10-15 mm. long, green or mottled with purple; seeds brown.

"Bradley Avenue clearing, June 4 and July 1, 1910; transplanted and specimens collected September 21, 1910 and May 13, 1911. A colony of several plants was found at this station."

There is in the Brainerd herbarium a specimen of this hybrid in flower collected by Dr. E. H. Eames in Fairfield, Conn., May 13, 1910, growing with both the parent species in a field bordering a brackish marsh. It answers well to Dowell's description of the plants found on Staten Island, N. Y.



Hybrid No. 21-Viola Britteniana × triloba

21. Viola Brittoniana X triloba, Brainerd.

Differs from V. Brittoniana in the direction of V. triloba in its large, less divided leaves with broad middle lobe, in pedicels one-half as long, in bearing pubescence on petiole and veins of leaf, and in having summer capsules dotted with brown. Differs from V. triloba in the direction of V. Brittoniana in being less pubescent, in bearing slim long-auricled cleistogamous flowers on ascending pedicels, and in its nearly green cleistogamous capsules.

This hybrid was discovered at Milltown, N. J., June, 1904, by House. A live plant sent me at that time (his No. 62), attained to a large size in the garden. In August, 1905, its leaves became ranker and less divided, its capsules bore only ½ the normal number of seeds found in capsules of either parent species, three capsules bearing only 37 seeds.

In March, 1904, I noticed in the National Museum two sheets of what seemed to be this hybrid from Stratford, Conn., Eames collector, May 24, 1893. On inquiry Dr. Eames wrote me that he remembered the plant as "a connecting link between V. palmata and V. atlantica, both of which grew there."

This hybrid was first published in Rhod. 8: 55, March, 1906, as "V. palmata × septemloba," specific names which were then everywhere misapplied.²

¹ Invalid name for V. Brittoniana Pollard, Bot. Gaz. 26: 332, 1898.

² See Torr. Club Bul. 37: 584-585, Dec., 1910; 38: 5-6, pl. 1, figs. 3 and 8, Jan., 1911.



Hybrid No. 22—Viola conspersa \times rostrata

22. Viola conspersa × rostrata Brainerd.

Spur of petaliferous flower intermediate between those of the parent species as to length and thickness, bright violet, 8-10 mm. long, often abruptly recurved at the tip; stipules 10-15 mm. long, fimbriate on the outer edge.

My first acquaintance with this hybrid was a living plant sent by Miller from Plainfield, N. J., June, 1906. This and its offspring were grown for several years. It was soon recognized as a hybrid, and its parentage was also apparent. From this stock were obtained specimens that were sent out as No. 31 in my Distribution 1910 of Violets of Eastern North America.

Soon after¹ another colony of this hybrid was found a half mile east of my home in Middlebury, Vt., growing with *V. conspersa* in a wet swale at the base of a ledge on which grew the other parent *V. rostrata*. From year to year since, the plants at this station have been under observation. Excellent specimens were collected as recently as May 29, 1923.

¹ Vt. Exp. Sta. Bul. 187, "Flora of Vermont", p. 227 (1915).



23. Viola cucullata × fimbriatula Brainerd, Rhod. 6: 217. Nov., 1904.

Blades of leaf wider and larger than in V. fimbriatula, in this respect as in V. cucullata; peduncles, petioles and upper surface of blades

often finely pubescent or hirtellous as in V. fimbriatula, not glabrous as in V. cucullata; cleistogamous flowers sometimes subulate as in V. cucullata, sometimes sagittate as in V. fimbriatula, sometimes intermediate.

This hybrid was first found in Salisbury, Vt., along a trout brook that crossed a sterile pasture at the base of the mountains. Along the edge of the water and in moist hollows *V. cucullata* Ait. was common, with short petioles and peduncles when growing in the open, and with long petioles and peduncles when growing in the shade of alders. On the drier knolls back from the brook were colonies of *V. fimbriatula* J. E. Smith. Near them were noticed in May, 1904, plants with wider leaves and larger, less decidedly purple flowers, marked with a ring of dark-blue at the center. They were examined again the following August and some eight of the plants removed to the garden. The cleistogamous flowers and autumn fruit, as well as the foliage and the vernal flowers, revealed a plant midway between the two familiar species with which the anomalous plants were growing; but no capsule ripened more than four seeds.

A similar plant had been collected, August 16, 1903, in Cheshire, Mass., where V. cucullata and V. fimbriatula were common. This in the one capsule that matured had only three seeds, but numerous aborted ovules. V. Porteriana Pollard, collected May 31, 1897, at Bushkill Falls, Pa., 1897, with V. fimbriatula, turned out to be the hybrid here discussed. Gradually it transpired that the cross was not infrequent along the eastern slope of the Appalachian Mountains. The range of V. cucullata is "springs and cold bogs from Quebec to northeastern Georgia"; that of V. fimbriatula "hillsides and dry fields from Quebec to northeastern Georgia." One familiar with this tract knows that in this glaciated region "hillsides" and "springs" are often found in close proximity to each other. Thus the parent species are often cohabitant, and the hybrid not infrequent. Over 12 stations are represented in the Brainerd herbarium.

From a station discovered, May, 1906, along the outlet of a cold spring in the northeastern part of Middlebury, Vt., plants were transferred to the home garden and studied with their offspring for four years. From stock transplanted from Waca, Pa., was obtained No. 36 of my 1910 Distribution of Violets of Eastern North America; from plants brought from Oak Mountain, Tryon, N. C., was obtained No. 37 of this Distribution.

¹ Torr. Bot. Club, Bul. 24: 404, t. 314, Aug., 1897.



Hybrid No. 24—Viola cucullata \times nephrophylla

24. Viola cucullata × nephrophylla Brainerd, Rhod. 8: 50-51. March, 1906.

Like *V. nephrophylla* in its relatively narrow leaf-blade, less than two inches wide; like *V. cucullata* in the strongly clavate beard of its lateral petals; like *V. nephrophylla* in its ovoid cleistogamous flowers, not subulate as in *V. cucullata*; like *V. cucullata* in its glabrous spurred petals, not villous as in *V. nephrophylla*.

In September, 1904, eight or ten plants of V. nephrophylla were transferred to my garden in Middlebury, Vt., from the borders of a cold brook running through the farm of the late Chief Justice Loveland Munson in Manchester, Vt. When they flowered, May 15, 1905, one of the plants was taller than the others, more cæspitose, had less obtuse leaves and bore smaller flowers on longer peduncles. A few days later the Manchester station was revisited, and occasionally similar plants were found, especially where in wetter spots colonies of V. cucullata bordered those of V. nephrophylla. Several days later at Arlington, Vt., 12 miles farther south, in a boggy meadow where these two species grew together, another of these anomalous forms was found, seemingly a V. cucullata with violet-colored flowers and bearded spur-petal. Transferred to the garden this and the Manchester plants, as they developed through the summer, gave abundant evidence of their hybrid origin. They had a luxuriant growth, but their numerous cleistogamous flowers proved to be nearly sterile. The two parent species are closely related, Nos. 20 and 21 in the list of North America Violets, arranged according to affinities (Bul. 224, p. 13). Their habitat is also quite the same, namely: cold bogs and borders of streams. The Battenkill River running south through Manchester and Arlington is at the base of two of the highest mountains of western Vermont, and the valley has been long famous for its cold trout brooks.

This hybrid is not known to occur elsewhere either in Vermont or southward.



Hybrid No. 25—Viola cucullata imes palmata and parent species

25. Viola cucullata × palmata Brainerd, Rhod. 15: 115. July, 1913.

Leaves nearly glabrous, broadly cordate-ovate, lobes as numerous as in *V. palmata*, but shorter; cleistogamous flowers intermediate in form to those of the parent species, on elongate ascending peduncles; auricles long, slightly setulose, sepals otherwise glabrous; capsules bearing only few seeds.

The hybrid was sent by Miss A. M. Ryan from East Lyme, Conn., October 4, 1906.

A hybrid was published in Rhodora 8: 56, March, 1906, by the above name, but at that date V. triloba was known as "V. palmata var. dilatata"—a "three-lobed form" of V. palmata. See Torr. Club Bul. 37: 584-586, December, 1910.



Hybrid No. 26-Viola cucullata ×papilionacea

26. Viola cucullata × papilionacea Brainerd, Rhod. 8: 56. March, 1906.

Plants often luxuriant and cæspitose; petaliferous flowers mottled; cleistogamous flowers subulate as in V. cucullata, nearly or quite sterile; foliage quite glabrous and uncut, as in both parents.

My first acquaintance with this hybrid was in August 22, 1905, when I saw and obtained a plant that Bissell of Southington, Conn., had transferred to his garden from the wild. Two weeks later at East Lyme, Conn., I saw plants in cultivation by Miss A. M. Ryan. The luxuriant growth of the hybrid was such that from one plant 20 large specimens were made by Miss Ryan for distribution. On September 8, 1905, in company with Eggleston, I collected a specimen of the hybrid in a low woods on the line between New York City and Yonkers.

I place with these specimens one collected by House (No. 131) in low woods, North Takoma, D. C. (now Takoma Park), July 30, 1904; and labeled by him *V. cucullata*.

Two other stations where the hybrid was discovered later are: Northampton, Mass., Mrs. Emily Hitchcock Terry, 1906; Plainfield. N. J., September, 1906, grown in Middlebury for one year.



Hybrid No. 27—Viola cucullata × primulifolia

- 27. V. cucullata × primulifolia Brainerd, Rhod. 11: 115. June, 1909.
- V. lavandulacea Bicknell, Torr. 4: 130. September, 1904.

Regarding this remarkable hybrid we present both of the publications above cited in their chronological order. It is interesting and instructive to follow the stages by which the students of *Viola* after more than four years arrived at a correct view regarding the status of Bicknell's plant. His original description is as follows:

"Tufted from short compound rootstocks, rather pale green, glabrous or with traces of minute pubescence on the upper surface of the leaves: petioles slender, much elongated, becoming 15-23 cm. long; leaf-blades oval or ovate and obtuse to deltoid-ovate and acute, abruptly contracted or truncate at the base, often slightly decurrent and a little undulate along lower margins, obscurely crenate or sub-entire to crenulate-denticulate, mostly 2-5½ cm. long, 2-4 cm. wide, or finally as large as 7×5 cm.: peduncles 10-30 cm. high, finally much surpassing the leaves: flower pale lilac to lavender blue, the petals whitened and much narrowed basally, all or all but the two upper ones sharply dark-lineate, the lateral pair bearded with a scant tuft of short gland-tipped hairs, the others glabrous, the lower one notably shorter than the others; sepals glabrous, lanceolate or linear-lanceolate, often sub-falcate, obtusely purplish apiculate; cleistogamous flowers on elongated erect pedicels, linear-lanceolate, the narrow sepals obtuse, the auricles rather small; mature capsules not seen.

"Southwestern Long Island, in damp meadows. Collected at Rosedale (May 9, 1903), and at Woodmere (May 21, 1904). Type from Woodmere, in Herbarium New York Botanical Garden.

"Related to *Viola cucullata* and growing with it, but well set apart from any of the cucullata group by its ovate or deltoid strictly non-cordate leaves. By comparison with *V. cucullata* in the field the flowers are seen to be markedly different in color as well as in other characters."



In September, 1905, I saw a fine plant of V. lavandulacea in the garden at Bronx Park which at once suggested that it was a hybrid. It was completely sterile. Although it bore 50 or more cleistogamous fruits, not a seed could be found. Its relationship to V. cucullata was evident from its somewhat short and beardless spurred petal and elongated peduncles; but the other parent of the conjectured hybrid was a mystery, until the publication of V. Brittoniana \times lanceolata by Forbes threw a new light on the problem. Bicknell and myself were agreed that we were dealing with a second hybrid between a white and a blue violet. The marks of V. primulifolia were seen to be as conspicuous as those of V. cucullata, namely, the truncate and decurrent base of the leaf-blade, its obscurely crenulate margin, its numerous nearly parallel veins diverging from the midrib, and the narrowed base of the petals.

This interesting hybrid in 1909 became extinct. It disappeared at the original Long Island stations; for a while it grew in the Bronx Park Garden; and for two years at Middlebury. Possibly the hybrid may again occur in moist meadows along the Atlantic coast.

¹ Rhod. 11: 14, Jan., 1909.



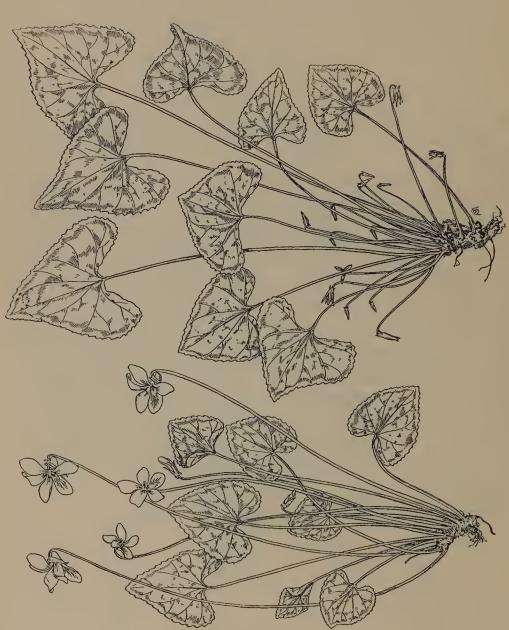
Hybrid No. 28—Viola cucullata \times sagittata

28. Viola cucullata × sagittata Brainerd, Rhod. 8: 52. March, 1906.

Blades of mature leaves deltoid and wide as in V. cucullata, but sharply and coarsely toothed at the base as in V. sagittata; beard of petaliferous flowers clavate, as in V. cucullata, but not in V. sagittata; cleistogamous flowers subulate with extended auricles as in V. cucullata, but not as in V. sagittata.

Specimens of this hybrid from two stations have been cultivated and carefully studied. The first was from Tinicum, Pa., 33 miles north of Philadelphia, on the west bank of the Delaware River, reported by Stone. Flowering and fruiting specimens are in my herbarium; also from a living plant grown for three years seedlings almost sterile were obtained. The second station is Montclair, N. J., five miles north of Newark. In June, 1907, living plants sent by Vreeland, and their offspring were grown for three years. Specimens, reverting in leaf-form to V. sagittata, were sent out as No. 38 of my 1910 Distribution of Eastern North American Violets.

¹ Proc. Nat. Acad. Sci., l'hila., p. 685, Oct., 1903. ² Stone No. 5141 and No. 5143, l. c., p. 685.



Hybrid No. 29-Viola cucullata × septentrionalis

29. Viola cucullata × septentrionalis Brainerd, Rhod. 6: 220. Nov., 1904.

Petioles and blades sparsely pubescent, not glabrous as in V. cucullata though less pubescent than in V. septentrionalis. Other characters differentiating the parent species in like manner intermediate in the hybrid; the sepals slightly hispidulous, not strongly so as in V. septentrionalis nor glabrous as in V. cucullata; cleistogamous flowers halfway between sagittate and subulate; spurred petal somewhat bearded, not beardless as in V. cucullata nor strongly bearded as in V. septentrionalis.

The plant is thus a striking example of a "blend hybrid." It was one of the earliest to be positively recognized, although it is necessarily restricted to northern regions, the home of V. septentrionalis, "the northern" violet. As early as the above publication it had been found at six stations, three in Addison County, Vt., and one each in Maine, New Brunswick and Prince Edward Island.

The corolla of this hybrid is large and of a beautiful violet-blue color inherited from both parents.

A specimen of the plant from the last mentioned station, collected by L. W. Watson in 1902, was published, by Greene as V. melissaefolia. In his description he refers to its large flowers "nearly an inch in diameter, sky-blue," and to the ciliolate sepals and recognizes its resemblance both to V. septentrionalis and to V. cucullata, or rather to their synonyms, V. nesiotica Greene² and V. prionosepala Greene³. But Greene never had any faith in the existence of violet hybrids. He is on record4 as saying "that to which any scientific mind should preclude * * * any hope of finding such is the simple fact that 99 out of 100 seeds of these plants are from flowers that having no corollas never open even their sepals * * * [and belong to] a group of plants which, as if intelligent entities, seem to use every thinkable natural precaution against cross fertilization."

¹Pitt. 5:103, Nov., 1902. ²Pitt. 5:102, Nov., 1902. ³Pitt. 5: 99, Nov.. 1902. ⁴Leaflets 214-5, June, 1906.



Hybrid No. 30a—Viola cucullata imes sororia

30. Viola cucullata × sororia Brainerd Rhod. 6: 222. Nov., 1904.

The characters of the hybrid plant present either a compromise of the contrasting characters of the two parent species or a reproduction of their common characters; not as pubescent as V. sororia and not as glabrous as V. cucullata; cleistogamous flowers not as subulate as in V. cucullata and not as obovoid as in V. sororia; leaves always cordate and flowers always violet-purple as in both parents.

This cross, like the preceding, was one of the earliest to be recognized and for a similar reason, its frequent occurrence in Western Vermont and Massachusetts, where the writer first studied *Viola* in the field. Specimens were collected in these stations with abundant evidence of their hybrid nature. They were growing with *V. cucullata* and *V. sororia*, their characters were a compromise between those of these two species and their infertility was apparent.

The first station was Cheshire, Mass., altitude 1,200 feet in moist soil, under a wild apple tree on the roadside. On May 20, 1903, I found here a clump of a strange violet bearing numerous large bluish flowers. I was at a loss whether to call it *V. cucullata* or *V. sororia*; and, hoping to remove the perplexity, I revisited the station, August 26, 1904. I found the plant bearing numerous capsules, all small, imperfect and few-seeded and concluded that the plant was a hybrid.

The second station was the west slope of Grand View Mountain, Addison, Vt., on mossy rocks, where were growing both *V. cucullata* and *V. sororia*. An intermediate plant was transferred to my garden in Middlebury, Vt., May 25, 1904, where its sterile, cleistogamous flowers on July 24 revealed its hybrid character.

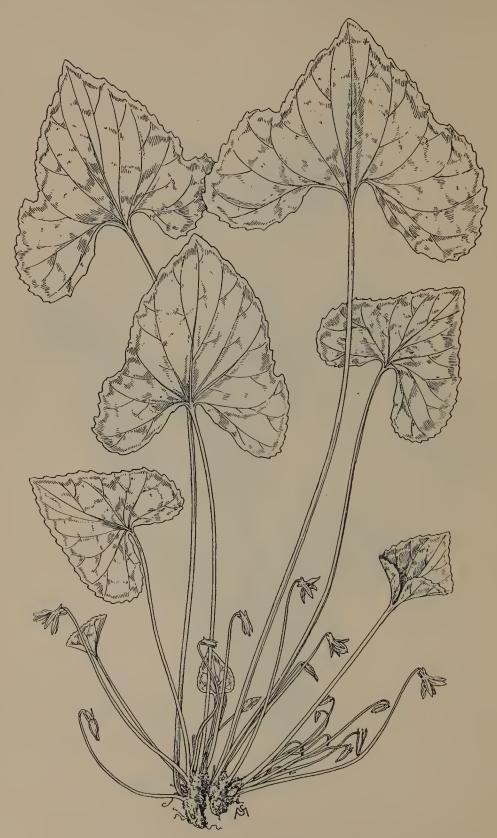
The third station was a cold spring at the base of the quartzite mountain in northeastern Middlebury, growing under *Juniperus virginiana* L. Seedlings from this appear in Nos. 41 and 42 of my Violet Distribution, 1910. The hybrid has since been received from Niantic, Conn., Long Island and Rochester, N. Y., and from the vicinity of Milwaukee, Wis.



Hybrid No. 30b—Viola cucullata \times sororia



Hybrid No. 31a-Viola cucullata × triloba



Hybrid No. 31b—Viola cucullata imes triloba

31. Viola cucullata × triloba Brainerd, nom. nov., Rhod. 15: 115. July, 1913.

V. cucullata × palmata Brainerd, Rhod. 8: 56. March, 1906.

Leaves pubescent on petioles, and under surface of blade as in V. triloba, some cordate-ovate, others three-lobed with broad middle segment; offspring of hybrid reverting variously to the characters of the parents, some plants bearing only broad uncut leaves, other plants bearing only three-parted leaves, still others intermediate; in all offspring the cleistogamous capsules notably sterile.

This hybrid was first detected in a set of living plants sent in May, 1905, by Prof. Greenman as "V. palmata" from Granny Hill, Lexington, Mass. The anomalous plant was grown at Middlebury till June, 1906. It was quite sterile, but produced numerous slender cleistogamous flowers resembling those seen on V. cucullata \times sororia. On visiting the station I observed that about 20 rods away in a marshy meadow at the base of Granny Hill plants of V. cucullata were growing.

On September 1, 1905, a live plant of the same hybrid was sent by Miss A. M. Ryan from East Lyme, Conn. From this and its seedlings many plants were grown during the five subsequent years, many of them being reversionary forms with quite infertile cleistogamous capsules.

A plant of this hybrid from Bradford, Pa., was once sent to Slavin, Curator of Parks in Rochester, N. Y., from whom a characteristic specimen, collected July 19, 1910, was received and deposited in the Brainerd herbarium.

The specific name "V. palmata" used in Rhodora, March, 1906, was replaced by V. triloba, when in December, 1910, the distinction between the two species was pointed out in the Torr. Club Bul. 37:584-5.



Hybrid No. 32—Viola cucullata \times viarum

32. Viola cucullata × viarum Brainerd ined.

Contour of leaf-blades intermediate, some uncut and sub-cordate as in V. cucullata, others deeply divided with a broad terminal lobe as in V. viarum; petaliferous flowers much as in V. cucullata, broader than in V. viarum and none emarginate; cleistogamous flowers subulate as in V. cucullata; seeds olive-brown as in V. viarum.

A hybrid of especial interest appearing spontaneously in my garden in Middlebury in 1912, growing with the parent species.

The type of *V. viarum* Pollard¹ was collected in St. Louis, Mo., growing on a railroad embankment, a circumstance that suggested its name. The home of the species was probably the Ozark of Northern Arkansas. In August, 1905, B. F. Bush sent me an unnamed specimen from Eagle Rock, Mo., stating that the plant was common along the rocky banks of the White River. This I was able to identify with specimens of the original collection in my herbarium, distributed from the National Herbarium as No. 32 of North American Violaceae. The plant received from Mr. Bush in 1905, or its offspring, is still growing in the Middlebury garden.

In 1912 I discovered an anomalous plant in the bed of V. viarum. Its seeds were the seeds of V. viarum, but its cleistogamous flowers were those of V. cucullata. Its leaf-pattern was intermediate, some uncut blades, sub-cordate but not truncate; its petals much broader than those of V. viarum and not emarginate; its cleistogamous flowers in the latter part of August, intermediate and apparently sterile.

Another circumstance is deserving our attention: The parent species of this hybrid are nearly allied though in geographical range widely apart. It is by no accident—although hardly intentional—that in the list of North American Violets "arranged according to affinities," V. cucullata and V. viarum are in juxtaposition, as is also the case in the Britton and Brown Illustrated Flora 2:552, Nos. 15 and 16.

¹ Britton Man., p. 635 (1901). ² Vt. Sta. Bul., 224, p. 13 (1921).



Hybrid No. 33—Viola emarginata imes fimbriatula

33. Viola emarginata × fimbriatula Brainerd, Rhod. 8: 57-58. March, 1906.

Plants intermediate between the two parent species, or presenting sometimes the character of one and sometimes the character of the other; leaf-blades usually deltoid, truncate, obscurely denticulate or coarsely incised on the basal angles, and inheriting pubescence from *V. fimbriatula*.

Of the above named hybrid I have specimens from four stations. From Linden, N. J., living plants were sent by Eggleston and House, June 12, 1904, from which two sheets of the plant in fruit were obtained August 21. In shape of leaf, in pubescence and in capsules and cleistogamous flowers it is a marked compromise between the characters of the parent species.

The second collection consisted of 15 living plants sent by Holm, September, 1904, from near Brookland, Washington, D. C. These were cultivated until September, 1905, and gave admirable reversionary forms of the parental species, a detailed account of which is given in the Rhodora paper above cited.

The third station from which I received this hybrid is Chadds Ford, Delaware Co., Pa., Stone (No. 5149) July 5, 1903. It was determined as *V. fimbriatula*, but it matches exactly those above cited.

The fourth station is Skyland, N. C., where it was collected September, 1923, by Miss Susan D. Sheppard who kindly sent several specimens.



Hybrid No. 34—Viola emarginata \times Lovelliana

34. Viola emarginata X Lovelliana Brainerd.

Blades of hybrid leaf often intermediate between those of the parent species as respects contour and pubescence, sometimes inheriting the three-lobed leaves found in V. Lovelliana, but not in V. emarginata; capsules more or less infertile.

The two sheets of this hybrid in my herbarium show 12 plants collected April 2, 1908, at Edgewood near Muskogee, Okla., growing with the parent species, specimens of which were also collected at the same time and place.

At first sight these specimens might seem to be V. emarginata \times triloba; but the range of V. triloba does not extend so far southwest as Oklahoma, and in fact there is no satisfactory evidence that such a cross ever occurred.

The line-drawing (Bul. 224, p. 68) of *Viola emarginata* is based on a fruiting specimen from the same station as that of the hybrid, transplanted and grown in my garden in Middlebury.



Hybrid No. 35—Viola emarginata \times papilionacea

35. Viola emarginata × papilionacea House, Rhod. 8: 120. July. 1906.

Early leaves triangular, cucullate, cordate, glabrous, very small; flowers small, pale purplish-blue, about 1 cm. broad, with dark-blue center and conspicuous purple veins; later leaves large, triangular, truncate or shallowly cordate, pale green, margins crenate-serrate towards the apex, deeply dentate or cut-toothed at the base, capsules about 6 mm. long or less on ascending peduncles, abortive, those from the petaliferous flowers apparently never developing.—Takoma Park, D. C., August 25, 1904 (No. 334, type); also July 30, 1904, April 23, and October 4, 1905.

Three stations are represented in the Brainerd herbarium: 1. Ivy Hill Cemetery, Philadelphia, Brainerd collector, September 6, 1905. 2. Living plants transferred to my garden, September, 1905, from Milltown, N. J., found with both parent species. 3. Living plants transferred from Brookland, D. C., Theo. Holm donor, May, 1908, ex horto Middlebury, May 29, 1910.

In these specimens the characters of the hybrid as described by House are strikingly exhibited. The evidence of sterile capsules from the petaliferous flowers is most pronounced, and in the plants from Brookland, D. C., grown for two years, even the cleistogamous flowers seem blasted.



36. Viola emarginata × sagittata Brainerd Rhod. 8: 58. March, 1906.

Leaves glabrous as in both parents, the blades sometimes broadly deltoid as in V. emarginata; sometimes narrowly lanceolate as in V. sagittata; the basal lobes coarsely dentate, passing upward into smaller and more remote apiculate teeth; ovules often aborted even in petaliferous flowers, in apetalous, sterile and withering brown. Often associated with the parent species.

It is important in the study of this hybrid to have a correct idea of the "sagittata" leaf which, blending with that of *V. emarginata*, determines the form of the hybrid leaf.¹ The word "sagittata" (arrowshaped) is somewhat vague. Gray defines it as having the main body of the blade tapering upward to a point and the ears acute and turned downward as in the common *Sagittaria*.² This surely does not describe the leaf of *Viola sagittata Ait*. (See color-plate, Vt. Sta. Bul. 224, p. 64, spec. No. 25). Many of the old specific names are fanciful. *V. sororia* Willd. gets its name "sister violet" from a supposed resemblance to *V. odorata* L., *V. striata Ait*. probably is so called because of the purple lines, or striæ, on the spur-petal, found in many other species and not a distinguishing character.

Specimens of this hybrid in my herbarium are from the following stations:

- 1. Cedarhurst, Long Island, N. Y., Bicknell collector, July 26, 1902.
- 2. Chester County, Pa., Stone collector, No. 5144, June 21, 1903,³ called *V. emarginata Nutt*.
- 3. Terracotta, D. C., Holm collector, September 28, 1904.
- 4. Milltown, N. J., Eggleston and Brainerd collectors, August 20, 1904.
- 5. North Takoma Park, D. C., Hyattsville, Md., Glencarlyn, Va., House collector (see Rhod. 8: 120, July, 1906).

¹ See figs. 2940 and 2941, Britton and Brown Illustrated Flora 2: 553, April,

<sup>1913.

&</sup>lt;sup>2</sup> See figs. 234 and 235 in Ill. Fl. I: 100, 1913.

³ Proc. Acad. Nat. Sci., Phila., p. 685, Oct., 1903.



Hybrid No. 37—Viola emarginata \times septemloba

37. Viola emarginata × septemloba House, hyb. nov., Torr. 14: 1-3. Fig. 1. Jan., 1914.

Plant glabrous at flowering time, the leaves varying from deltoid to sagittate, the middle lobe of the blade elongated, the lateral lobes very narrow, the basal ones nearly at right angles to the middle lobe; summer leaves several-lobed, the middle lobe longest and largest; flowers large, pale blue in color (Gilmerton, Norfolk Co., Va., No. 4857, April 20, 1912). Growing with both parent species.

This hybrid has some resemblance to hyb. 15, Viola Brittoniana \times emarginata, first found in the District of Columbia, and figured in Rhodora 8: 120, pl. 71, July, 1906. It lacks, however, the stoutness of that plant, and in its more slender habit shows its relationship to V. septemloba.



Hybrid No. 38—Viola emarginata \times sororia

38. Viola emarginata \times sororia Brainerd.

Mature leaves ovate as in V. sororia, not deltoid as in V. cmarginata; basal lobes incised with triangular teeth at the base, the sinus deep and narrow; under surface of leaf-blades less pubescent than in V. sororia, but not glabrous as in V. emarginata, margins ciliolate.

My specimens consist of three plants collected by E. J. Palmer along a railroad track in a dry prairie at Carthage, Mo.—two in petaliferous flower (No. 3343) April 9, 1911 and one (No. 3376) with fruit and long slender apetalous flowers May 14. Both fruiting capsules and apetalous flowers are decidedly infertile.

The plant was first determined as V. fimbriatula, doubtless because of its marked pubescence; but the town of Carthage (44 miles north of south line of Missouri, and 17 miles east of west line), is 700 miles west of the range of V. fimbriatula, a species having a truncate base not deeply and narrowly cordate, as in the hybrid.

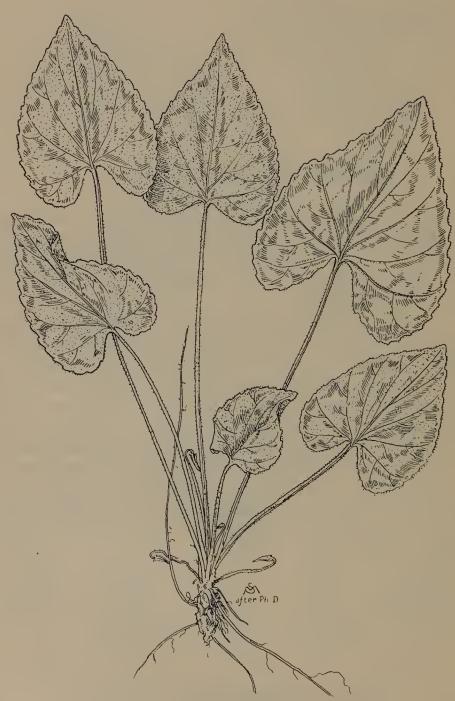


Hybrid No. 39—Viola emarginata imes Stoneana

39. Viola emarginata \times Stoneana Brainerd.

Contour of leaf-blades in the hybrid specimen collected September 29, 1905, of two patterns: one coarsely toothed at the base as in V. emarginata, the other three-parted, the segments 2-3-cleft, the middle division the widest, quite as in V. Stoneana; plant glabrous throughout as in both parent species.

This hybrid was collected by me at Ivy Hill Cemetery, Philadelphia, Pa. For several years it was grown at Middlebury and many off-spring raised from its seed. The 18 capsules obtained from the original plant were infertile; the four least infertile yielded only 156 seeds instead of the normal 240; the remaining capsules, 14 in number, yielded an average of $7\frac{5}{7}$ seeds, only $13\frac{1}{3}$ percent of the normal number. Furthermore, the plants obtained from the sowing of these seeds were markedly variable in outline: some three-divided or three-parted with the segments 2-3-cleft, as in V. Stoneana; others broadly ovate or deltoid, base truncate and decurrent, the lower margin coarsely toothed, as in V. emarginata; and, lastly, with these were to be found still others of intermediate pattern.



Hybrid No. 40—Viola fimbriatula \times hirsutula

- **40.** Viola fimbriatula × hirsutula Dowell Bul. Torr. Cl. 37: 175, pl. 15. April, 1910.
- V. fimbriatula × villosa House, Rhod. 8: 121. July, 1906.

"Plant pubescent, low, with erect or ascending rootstock. Leafblades thick and firm, dark green above, ovate, acute, cordate, crenateserrate, ciliate and oppressed-pubescent, with the characteristic hairs of *V. hirsutula* on the upper surface; petioles one to two times as long as the blades. The imperfectly developed cleistogenes sagittate, small, on short decumbent or ascending puberulent peduncles; calyx-lobes purplish, lanceolate, with rather long ciliolate auricles."

Woods west of Egbertville, Staten Island, N. Y., in the *V. hirsutula* patch, August 23, 1909 (6007). Bul. Torr. Cl. 37: 167, April, 1910.



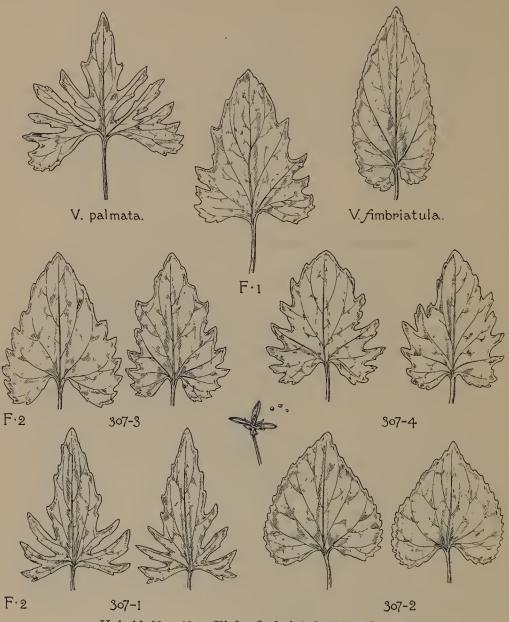
Hybrid No. 41—Viola fimbriatula \times latiuscula

41. Viola fimbriatula × latiuscula Brainerd.

Plants inheriting variously the contrasting characters of the two parents; some pubescent as in V. fimbriatula, others glabrous as in V. latiuscula; some with broad deltoid leaves as in V. latiuscula, others with ovate leaves as in V. fimbriatula; some having green capsules as in V. fimbriatula, others purple-spotted capsules as in V. latiuscula.

The type of *V. latiuscula* was collected by Eggleston in shady well-drained soil on the lower slopes of Twin Mountains, West Rutland, Vt., May and July, 1902. It was later found in several other stations in Western Vermont and adjacent New York, and in Rhodora 24: 184, September, 1922, it is reported from New Hampshire. As now known, its southwestern limit is Bradford, McKean Co., Pa. (See Torr. Club Bul. 37: 590, Dec., 1910.)

Its hybrid, with *V. fimbriatula* was discovered, September, 1906, in sandy soil on the grounds of Fort Ethan Allen, Vt. The plant was transferred to my garden in Middlebury and during the two subsequent years numerous offspring were obtained from its seeds that displayed the characters above described.



Hybrid No. 42a—Viola fimbriatula × palmata

42. Viola fimbriatula × palmata Brainerd, Rhod. 15: 114. June, 1913.

Leaf-blades ovate in outline, subcordate, obtuse, 3-5-lobed or cleft on either side chiefly below the middle, finely pubescent especially on the petioles and along the veins of the lower surface; flowers, capsules and peduncles intermediate between those of the parent species; plants quite infertile; offspring diversiform—some with leaves like those of the hybrid parent, others with leaves uncut as in V. fimbriatula, and still others with deeply lobed leaves as in V. palmata, in all cases the width of leaf being intermediate.



Hybrid No. 42b— $\dot{\text{Viola}}$ fimbriatula \times palmata

Specimens of this hybrid in the Brainerd herbarium are as follows: Rocky woodland, Yonkers, Westchester Co., N. Y., Brainerd collector, September 9, 1905; East Lyme, Conn., Miss A. M. Ryon, October, 1905; Sylvanbeach, Oneida Co., N. Y., House 1244 (in part), July 11, 1905; Palmer's Glen, N. Y. [near Rochester?] J. Bishop collector, 1909; Tryon (alt. 760 m.) N. C., Brainerd, April 21, 1910; Spring Valley, Rockland Co., N. Y., Miss E. M. Kittredge, May 26, 1911.



Hybrid No. 43—Viola fimbriatula \times papilionacea

43. Viola fimbriatula × papilionacea Brainerd, Rhod. 8: 54. March, 1906.

Cf. Rhod. 6: 218-219, November, 1904.

Blades of mature leaves wider than in V. fimbriatula, narrower than in V. papilionacea; lobes often sharply toothed as in V. fimbriatula, not merely crenate-serrate as in V. papilionacea; plants usually pubescent as in V. fimbriatula, but often quite glabrous as in V. papilionacea.

This hybrid was a source of perplexity to American botanists from 1900 to 1906. Varying opinions regarding its status were advanced by Greene, Stone and House. Greene, when botanist of the Catholic University at Washington, seems to have been the first to take notice, in 1900, of this abnormal plant. In Leaflets 1: 187, February, 1906, he tells about once observing in a colony of true V. fimbriatula a plant differing from all the others, which, in 1900, he transferred to his garden, where it flourished for three years. Meanwhile seven or eight plants from self-sown seeds sprang up around it, one of which was a perfect "revert" to V. fimbriatula without shadow of approach to its immediate parent, while the other six or seven seedlings were as precisely true to this parent. It was found not to be rare in the District of Columbia and soon after a dried specimen of the same thing was sent in by Stone (No. 5150) from Philadelphia for Greene to determine, who sent in his manuscript name for it, V. aberrans. Stone published this as "V. fimbriatula aberrans (Greene); essentially a long petioled V. fimbriatula, with broad, cordate, somewhat cucullate leaves, without strong basal teeth and usually somewhat pubescent." In reply to my inquiry regarding his No. 5150 Stone wrote: "I think V. papilionacea did grow in the vicinity; V. fimbriatula was there in abundance; and my surmise was that my plants were hybrids between the two." Greene, however, had no faith in the possibility of hybridism in Viola; the anomalous forms he considered "mutates."2

The 22 specimens in my herbarium show that the hybrid is found in Connecticut, New York, New Jersey, Pennsylvania, Maryland, and District of Columbia. It may be looked for farther southwest to the mountains of North Carolina.

¹ Proc. Acad. Nat. Sci., Phila., p. 683, pl. 37, figs. 4-6, Dec., 1903. ² See Leaflets 1: 187, Feb., 1906.



Hybrid No. 44—Variable leaves of Viola fimbriatula imes sagittata

44. Viola fimbriatula × sagittata Brainerd, Rhod. 8: 57, pl. 68. March, 1906.

Plants with foliage sometimes quite like that of one or the other of the parent species rather than a compromise of their divergent characters; the leaf-blade sometimes broad, as in V. fimbriatula; sometimes narrow as in V. sagittata; sometimes glabrous as in V. sagittata; sometimes pubescent as in V. fimbriatula; the basal lobes sometimes sharply incised as in V. fimbriatula, sometimes coarsely 2-3 dentate as in V. sagittata, these various forms appearing independently of each other, as in mathematical permutation.

This hybrid was first collected by Greene in Anne Arundel County, Md., in the spring of 1898 and published as *V. conjugens* in Pitt. 4: 3-4, January, 1899. About a year later a clump of it was transferred to his garden. Its only offspring, self-sown, differed so much from the original plant that in February, 1906¹ he thought it a "mutate," rather than a hybrid, which, in his opinion, was an impossibility.

As early as 1904, this anomalous plant had attracted attention at several stations, from the vicinity of Boston to New Brunswick, N. J. Four of these stations I visited, as reported in my Rhodora paper. Subsequently, live plants from several other stations and their seedlings were grown in my garden. They ripened plentiful seeds but the plants raised from these seeds reverted variously to the characters of V. sagittata and V. fimbriatula as above described.

This behavior is analogous to that found in V. tripartita and its variety with uncut leaves. The species and variety interbreed and produce a progeny whose leaves are various recombinations of the unlike parental forms. In like manner, V. lobata, of the Pacific slope, has a distinct variety with deltoid or rhombic-ovate leaves. When the species and its variety interbreed, the leaves of the offspring differ in various ways from the leaves of the parents. We have a noted example of this dimorphism in *Phaseolus multiflorus*, a native American bean, having an albino variety with which it interbreeds and reproduces numerous intergradient forms.

¹ Leaflets 1: 186-7.



Hybrid No. 45—Viola fimbriatula \times septentrionalis

45. Viola fimbriatula × septentrionalis Brainerd, Rhod. 6: 215-7, pl. 58. Nov., 1904.

Width of leaf-blade intermediate between the broadly cordate leaf of V. septentrionalis and the lanceolate truncate leaf of V. fimbriatula; capsules of apetalous flowers somewhat green and oblong as in V. fimbriatula but usually mottled and globose as in V. septentrionalis, markedy infertile bearing on the average only $\frac{1}{8}$ the normal number of seeds, the other $\frac{7}{8}$ being represented by aborted ovules.

This, the first violet hybrid in America to receive recognition, is described at length in the paper here cited, and illustrated by Mathews' admirable drawing. The range of the hybrid is restricted to that of V. septentrionalis, the "northern violet," from Newfoundland west to Ottawa and south through New England to northern Pennsylvania. But I am not aware of the occurrence of the hybrid south of Massachusetts. It is readily recognized by the closely ciliolate sepals inherited from V. septentrionalis and the pubescent foliage inherited from V. fimbriatula. The mark of hybridity is as usual found in the sterility of the capsules.

Before the date of its publication the hybrid had been often collected, passing sometimes as V. fimbriatula; sometimes as V. sororia; sometimes sent without name, once from Orono, Me., Fernald No. 2706, September, 1898; once from Hawley, Franklin Co., Mass., Forbes, dry open pasture, alt. 2,200 feet, August 18, 1904.

It was by the discovery of this hybrid in Prince Edward Island that the range of *V. fimbriatula* was found to extend farther northeast than southern Maine and New Brunswick.



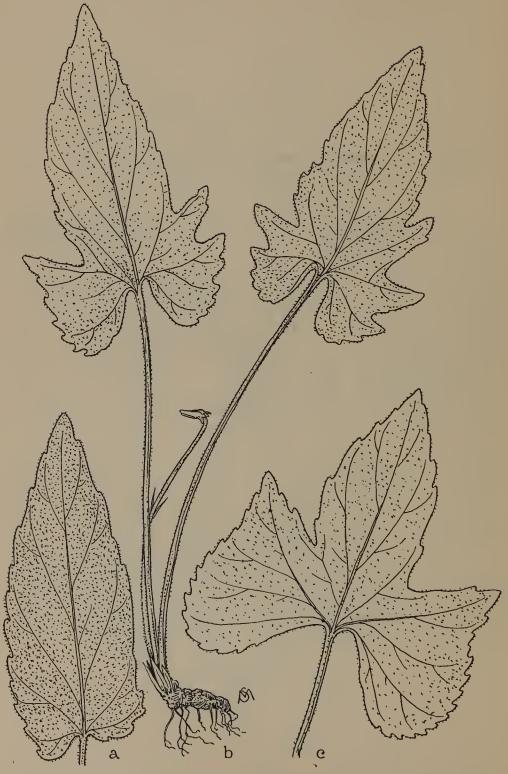
Hybrid No. 46—Viola fimbriatula imes sororia

46. Viola fimbriatula × sororia Brainerd, Rhod. 6: 218. Nov., 1904.

A hybrid displaying the narrow leaves and prominent stipules peculiar to V. fimbriatula, and the broad leaves and brown-spotted capsules peculiar to V. sororia.

This hybrid first attracted my attention in May, 1902, growing at the base of a ledge in a pasture at Middlebury, Vt. The foliage and the color of the flowers at once distinguished it from plants of V. fimbriatula with which it was intermingled; at the same time its narrow leaves and prominent stipules separated it from V. sororia, which grew about 20 feet distant. I took but few specimens as the colony was not a large one; some of these I sent to Pollard, querying if it might not be a hybrid. He considered it more probably a new species. Later the fruit showed unmistakable marks of V. sororia. The hybrid much resembles V. fimbriatula \times septentrionalis; but the less ciliate sepals and their smaller oppressed auricles serve to distinguish it. It is less sterile than most hybrids, but I never found a capsule that contained more than half the normal number of seeds.

The only other station for this hybrid, that I know of, is Hempstead, Long Island, N. Y., Miss Mulford collector, dry woods, May 18, 1904; sent as *V. sororia*. The range and habitat of the parents of the hybrid are much the same, and one naturally queries if it has not been overlooked because of its resemblance to other violets.



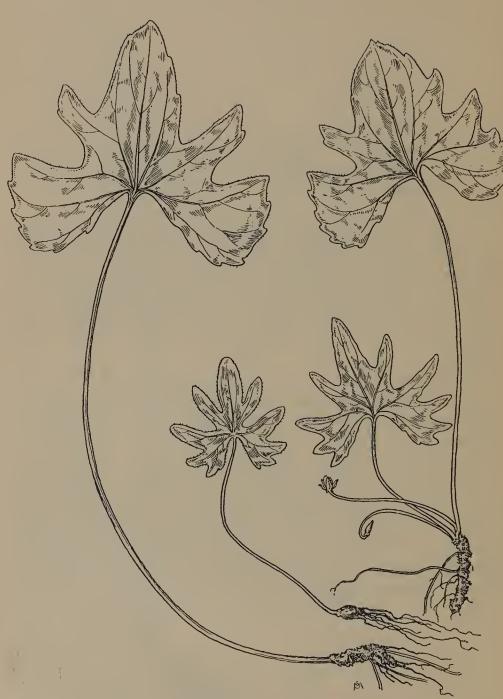
Hybrid No. 47—Viola fimbriatula imes triloba and leaves of parent species

47. Viola fimbriatula × triloba Robinson in hb., Rhod. 8: 53, pl. 70, March, 1906, as amended by Brainerd, Rhod. 15: 114, June, 1913.

Aestival leaves ovate-oblong in general outline, acute or pointed, with one to three incised lobes on either side below the middle, clothed with minute soft pubescence; cleistogamous flowers intermediate between those of parent species; capsules somewhat dotted with brown, infertile. "Crevices of rocks in open woods with parent forms, Granny Hill, Lexington, Mass., September 20, 1903," Robinson and Greenman collectors.

Robinson first called my attention to this hybrid, May, 1905. Greenman sent me some 20 living plants, and the following August I visited the station. The leaves were found to vary in relative width and lobation, as do those of V. triloba, and those produced in late summer were often uncut or only slightly lobed.

The hybrid has since been found in several other stations: two in New Hampshire, two in Connecticut and one in New York, six miles east of Rochester. Specimens from these stations are in the Brainerd herbarium. Attention is called to plate 70 above cited as exhibiting the compromise in the hybrid leaf between the leaves of the parent species. Here for "palmata" read *triloba*.



Hybrid No. 48—Viola hirsutula \times palmata

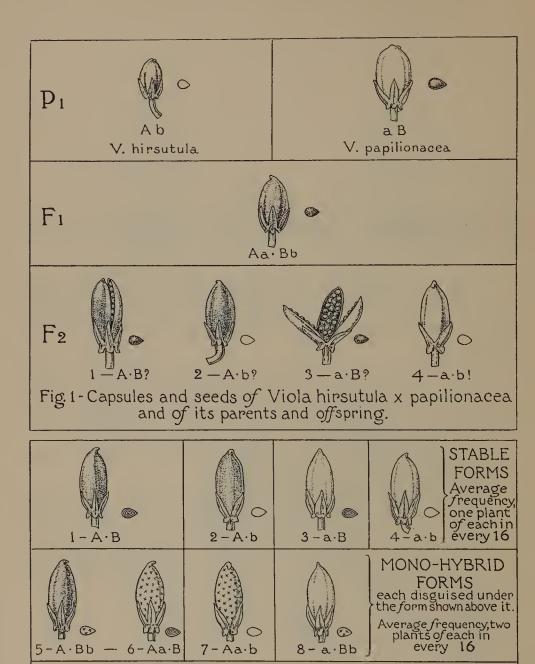
48. Viola hirsutula × palmata Brainerd, Bul. Torr. Cl. 39: 96. March, 1912.

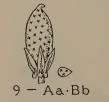
Plant small, cespitose; leaves all palmatifid, the incisions becoming shorter toward the base; the blades somewhat pubescent beneath, finely ciliate and bearing minute white hairs along the veins above; capsules nearly sterile.

Only one plant of this hybrid was found by Miller in an open woods near Plainfield, N. J., May, 1906, growing near both supposed parents. This was transplanted to my garden in Middlebury and grown during the six subsequent years. It was so sterile that I was never able to secure sufficient seed for a sowing, but a number of plants were obtained by dividing the rootstock.

There could be no doubt as to its hybrid origin, and the evidence as to the parent species was to be seen in the flowers and in the contour and pubescence of the foliage, these having characters intermediate between those of V. palmata and V. hirsutula. Especially marked was the presence, only on the upper leaf-surface, of the minute silvery hairs peculiar to V. hirsutula, as the specific name indicates.

¹A second station for this hybrid was found by Miss Cicely Sheppard at Skyland, N. C., Aug. 20, 1923, growing with both parent species.





DI-HYBRID FORM always disguised as A·B Average frequency, 4 plants in every 16

Fig. 2-Color forms in offspring of Viola hirsutula x papilionacea

49. Viola hirsutula × papilionacea Brainerd Rhod. 9: 98. June, 1907.

V. papilionacea × villosa House, Rhod. 8: 121. July, 1906. Cf. Rhod. 9: 211-216, November, 1907.

House thus described the hybrid in Rhodora, July, 1906: "Mature leaf-blades oblong-ovate to suborbicular, obtuse, obscurely crenate toward the apex, more conspicuously serrate at the base, cordate, deepgreen, nearly glabrous, especially beneath, but the blades more or less pubescent above with whitish hairs, capsules abortive on spreading peduncles."

In view of subsequent data, I would offer this supplement: Leafblades of hybrid plant in contour intermediate between the parent species; in pubescence, on the under surface glabrous as in both parents; on the upper surface more or less silvery pubescent as in V. hirsutula.

This hybrid was late in securing a correct name because *V. hirsutula* had no valid name until published at the same date and on the same page as the hybrid, June, 1907. But no violet hybrid has been cultivated with more interesting results.

It first attracted my attention in June, 1905, when I received live plants from Stone from two stations in Philadelphia. Ivy Hill Cemetery (Stone No. 5100) and Sherwood (Stone No. 5102). These were named *V. villosa* cordifolia Nutt.¹ and illustrated in Proc. Acad. Nat. Sci., Philadelphia, pl. 31, figs. I, a, b, c, October, 1903. The live plants from Stone, cultivated for two seasons, showed impaired fertility and their seedlings displayed strikingly diverse characters as to size of leaf, color of capsules and color of seeds. In the summer of 1907 I was able to show that in respect to color of capsules, respectively purple and green, and to color of seeds, respectively buff and dark-brown, this hybrid illustrated Mendel's law of dominance. For details of these experiments the reader is referred to the text above cited, Rhod. 9: 211-216.

It should be kept in mind that for many years V. villosa Walt (a plant of the coastal plains ranging south and west from the mouth of Chesapeake Bay) was confused with V. hirsutula Brainerd, a plant of the Piedmont upland plateau, ranging from Bridgeport, Conn., along the Appalachian Mountains to northern Alabama.

^{· &}lt;sup>1</sup> Genera I, p. 148 (1818).



Hybrid No. 50—Viola hirsutula \times sororia

50. Viola hirsutula × sororia Dowell, Bul. Torr. Cl. 37: 176, pl. 16. April, 1910.

"Dark green, pubescent, two dm. tall. Leaf-blades broadly ovate, obtuse, cordate or somewhat reniform, upper surface appressed pubescent with the characteristic hairs of *V. hirsutula*, lower surface pubescent on the veins; margin ciliate, crenate; petioles ascending, pubescent, one to three times as long as the blades. Cleistogenes not fully developed, small, on prostrate or decumbent peduncles; calyx purplish, with short ciliolate auricles.

"This resembles the corresponding cross with V. papilionacea, differing chiefly in having pubescent petioles and lower surfaces of leaves."

Plate 16 above cited well represents the leaves of this hybrid in respect to form and pubescence. As early as May 8, 1904, House collected it at Milltown, N. J. It then passed as V. villosa as did all forms of what is now known as V. hirsutula.

I have specimens from three other stations in New Jersey; from Rockville, D. C., E. S. Steele, collector, May 12, 1901; and I collected it at Biltmore, N. C., April 19, 1908, and at Tryon, N. C., April 16, 1909.



Hybrid No. 51—Viola hirsutula \times Stoneana

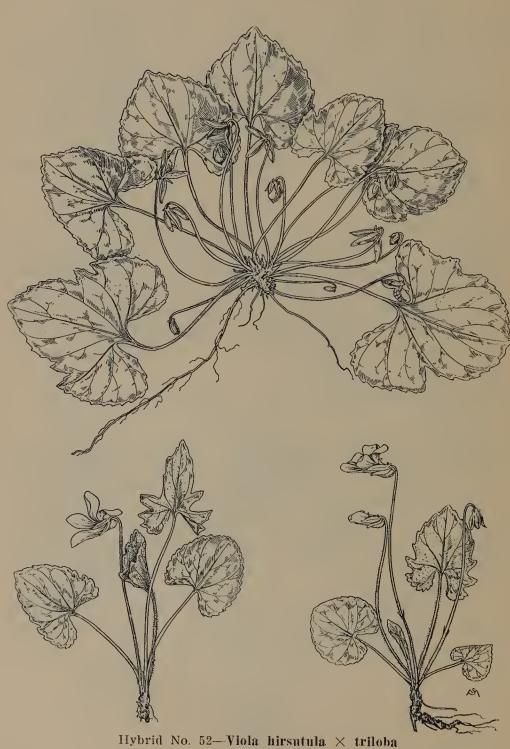
- 51. Viola hirsutula × Stoneana Brainerd, nom. nov., Bul. Torr. Cl. 39: 96. March, 1912.
- V. Stoneana × villosa House, hyb. nov., Rhod. 8: 121, pl. 72. July, 1906.

"Growing in dense, matted clumps, the leaves at flowering time spreading on petioles 5 to 10 cm. long, pubescent above with the silvery whitish hairs characteristic of V. villosa and even more strongly ciliate on the margins than V. Stoneana, nearly glabrous beneath and somewhat shining; size of plant and lobing of the mature leaf-blades exactly intermediate between the two species and growing with them. Flowers intermediate in color between the blue of V. Stoneana and the deep purple of V. villosa.

"Hyattsville, Md., May 5, 1905 (No. 685, type), June 4, 1905 (No. 935a)."

This description of House and the accompanying plate (72) are admirable. Duplicates of the specimens collecting in 1905 are in the Brainerd herbarium. The only needed emendation is to substitute for "V. villosa," V. hirsutula, not published till June, 1907. I find also in my herbarium a specimen that I collected, September 6, 1905, Ivy Hill Cemetery, Philadelphia, Pa., when with Stone. Neither of us could then name the plant, but on the same sheet are two specimens of V. Stoneana.

In 1908 I received from Theo. Holm live plants from Brookland, D. C., which with their offspring I cultivated for three years with most satisfactory results as to reversionary forms.



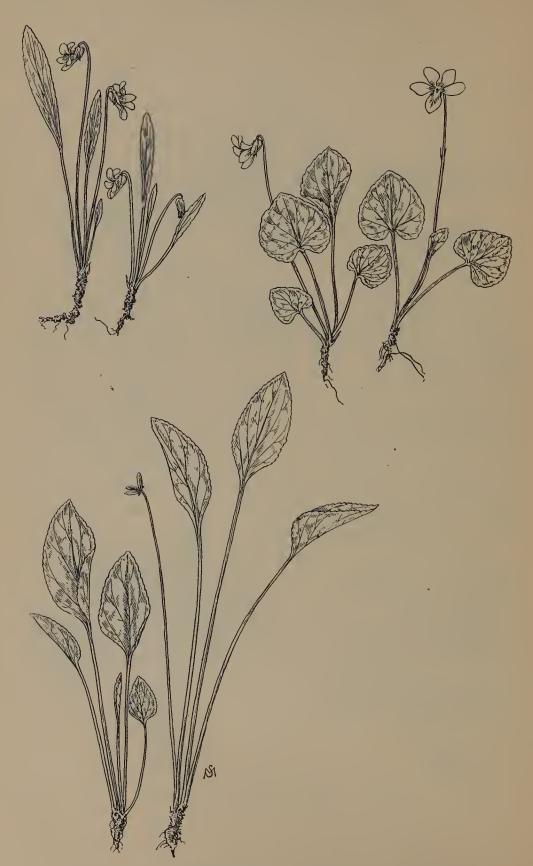
- 52. Viola hirsutula × triloba Brainerd, nom. nov., Bul. Torr. Cl. 39:95. March, 1912.
- V. palmata × villosa Brainerd, Rhod. 8: 56. March, 1906. See also House, Rhod. 8: 121. July, 1906.

Plants reverting in various ways to the characters of one or the other parent species; some leaf-blades lobed as in V. triloba, others uncut as in V. hirsutula; most displaying the silvery pubescence of V. hirsutula on the upper surface and the villous pubescence of V. triloba on the lower surface.

In the first publication of this hybrid, March, 1906, the untenable names of the parent species prevalent at that time, had to be used, for V. hirsutula was not published till June, 1907,1 and V. triloba not separated from V. palmata till December, 1910.2 But the hybrid had been collected by Pollard as early as 1899 at Biltmore, N. C., and distributed from the National Herbarium. Also a plant-Stone's No. 5107 collected at Sherwood, Pa., May, 1903 and called "V. palmata dilatata Elliot" is evidently our hybrid.

This beautiful plant is of frequent occurrence from northern New Jersey to the mountains of North Carolina and eastern Tennessee. A most interesting colony of a hundred or more plants was found at Morristown, Tenn., on a tract of woodland recently cleared and worked to be made an addition to a cemetery. From these I have raised unlike offspring, some with uncut leaves, others with leaves mostly 3-lobed.

¹ Rhodora 9: 98. ² Bul. Torr. Cl. 37: 584-585.



Hybrid No. 53—Viola lanceolata \times pallens and parent species

53. Viola lanceolata × pallens House, Bul. N. Y. St. Mus. 243-244, p. 26. March-April, 1921.

"This was taken at first for V. primulifolia because of its broad leaves. Further observations of it during 1921 showed that the petaliferous flowers were always sterile, the flower and its peduncle soon withering and never developing capsules. The leaves simulate those of the more southern V. primulifolia but are entirely smooth and in texture more like those of V. pallens.

Shore of Lake Harris near Newcomb, N. Y., growing with *V. pallens* and *V. lanceolata* House (7254). June 6-12, 1921; August 1-10, 1921."

In a letter of June 13, 1923, House writes: V. lanceolata \times pallens passed under my observation for nearly a season, as a northern form of V. primulifolia, before I suspected its real position, which became apparent as soon as I began to look for mature capsules. As yet I have not found any developing from flowers.

The illustrations on the opposite page were drawn from plants kindly furnished by House.



Hybrid No. 54—Viola lanceolata \times primulifolia

54. Viola lanceolata × primulifolia Dowell Bul. Torr. Cl. 37: 176, pl. 17. April, 1910.

"Plant taller and more slender than V. primulifolia, and in general appearance intermediate between this and V. lanceolata. Leaf-blades ovate to lanceolate, acute or obtuse, decurrent on the petiole, margin crenate with low teeth, the points of which are incurred. Early flowers on long slender peduncles equal to or longer than the petioles; capsules green, about 8 mm. long; seeds brown."

Specimens were found at three different stations; "some transplanted at home showed the same intermediate character at the end of the season." The plate is an admirable illustration of the characters noted in the description.



Hybrid No. 55—Viola Langloisii \times rosacea

55. Viola Langloisii × rosacea Brainerd, hyb. nov.

Blades of mature leaf broadly deltoid, crenate-serrate, glabrous, more like those of V. rosacea than like those of V. Langloisii; cleistogamous flowers on ascending peduncles as in V. Langloisii, not prostrate as in V. rosacea; capsules of normal length but infertile, 17 yielding only 96 seeds.

My only specimen of this hybrid was found in Crowley, La., March, 1910, on the dry soil of the Fair Ground and transferred to my garden in Middlebury where it grew until the following August.

Both parent species were frequent in Crowley—V. Langloisii on the wet shady margins of bayous, V. rosacea in dry open woodlands or along well-drained borders of bayous.



Hybrid No. 56—Viola latiuscula imes sororia

56. Viola latiuscula × sororia Brainerd, hyb. nov.

Leaf-blades broadly deltoid as in V. latiuscula; peduncles, petioles and under surface of blades, villous-pubescent as in V. sororia, but not in V. latiuscula; other characters are for the most part those common to the nearly allied parent species.

Specimens in the Brainerd herbarium are from three stations:

- (1) Salisbury, Vt., on the mountain road from Lake Dunmore to East Middlebury. The hybrid was collected in May and July, 1903, and also typical *V. latiuscula* growing with it. In 1907 collections were again made, and live plant transferred to the home garden for a study of its offspring.
- (2) Twin Mountains, West Rutland, Vt., the type station for V. latiuscula, collected the summer of 1902. Here also, the hybrid was collected by Eggleston July 30, 1903, but sent me as V. sororia.
- (3) A moist pasture slope near Hoosic Junction, N. Y., 13 miles northwest of Williamstown, Mass., where I collected it May 19, 1903. I labeled the plant *V. sororia*, though at the same place and time I recognized and collected typical *V. latiuscula*, and noted on the *sororia* label: "Growing with *V. latiuscula* and like it in deltoid outline of leaf, in reddish color of early leaves and in violet petals."



Hybrid No. 57—Viola latiuscula \times triloba

57. Viola latiuscula × triloba Brainerd, hyb. nov., Bul. Torr. Cl. 39: 94-95. March, 1912.

Leaves moderately 3-5-lobed, sparsely pubescent on the petioles and veins of the young leaves; capsules about 8 mm. long, maturing 10 or 12 brown seeds; progeny heterogeneous.

For my acquaintance with this hybrid I am indebted to the discernment and diligence of Slavin of the Park Department of the City of Rochester, N. Y. On June 19, 1909, he sent me from Salamanca, N. Y., six odd-looking plants, all glabrous; four with leaves somewhat lobed, subcordate-ovate, blunt-pointed; two with leaves uncut. As they flowered and matured the following season, I detected certain marks of V. latiuscula: a crimson tinge in the early spring foliage, and a granular roughness along the upper edges of the petiole. At my request Mr. Slavin revisited the station for further collections July 6, 1910, and sent me in the autumn an excellent suite of the various forms to be seen in that colony. For a better apprehension of their relation to each other, I borrow some of the symbolism of Mendel. For brevity he uses letters instead of phrases, somewhat in this fashion:

Let A = cut-leaved

Let B = pubescent

Let b = glabrous

Let Aa = with leaves somewhat cut

Let Bb = somewhat pubescent

All of these six characters are found in the above described hybrid or in the parent species; in the offspring of the hybrid they should be redistributed in all possible combinations. It is evident that each one of the three characters in the first group may combine with each of the three in the second group, making in all nine different combinations. These are given in the following table, the asterisk after any form denoting its occurrence at the Salamanca station.

1 2	A -	B	*	Reversion to typical V. triloba. New and stable form, glabrous V. triloba.
3		Bb	*	Cut-leaved form, hybrid as respects pubescence.
4		B	*	New and stable form, pubescent V. latiuscula.
5	a <	b	*	Reversion to typical V. latiuscula.
6		Bb		
7		B	*	Pubescent form, hybrid as respects lobation.
8	Aa	b	*	Glabrous form, hybrid as respects lobation.
9		Bb	*	Dihybrid, V. latiuscula × triloba.

The one form lacking should be a somewhat pubescent plant with uncut leaves. The proof that we have here a colony of V. latiuscula \times triloba will be convincing to one familiar with the behavior of hybrids.



Hybrid No. 58—Viola Lovelliana \times papilionacea

58. Viola Lovelliana × papilionacea Brainerd ined.

Pubescent on petioles and under surface of leaf-blades as in V. Lovelliana, not glabrous as in V. papilionacea; in contour of blades intermediate between the two parents.

This hybrid was first collected April 2, 1908, in an open woodland near Muskogee, Okla., growing with typical V. Lovelliana; it was then suspected to be a hybrid of this with V. papilionacea. Two years later, I again collected the hybrid at the same station and shipped home living plants for a study of its fruit in autumn. A plant dried for the herbarium September 2, 1910, presents a striking reversion to V. papilionacea in width of leaf-blade and in lack of pubescence. It has several cleistogamous flowers and capsules, the capsules containing only aborted ovules.



Hybrid No. 59—Viola missouriensis \times sororia

59. Viola missouriensis × sororia Brainerd.

Blades of secondary leaves broadly deltoid with concave crenate-serrate margins as in V. missouriensis, but notably pubescent on the under surface and on the petioles as in V. sororia.

I have only two specimens of this hybrid, one from Baldwin, Kan., Rufus Crane (No. 1390) collected May 29, 1913, and one grown at Middlebury from plants sent by B. F. Bush from Courtney, Mo., May, 1904, and dried September 19, 1905. Both the native stations are near Kansas City, Baldwin being 38 miles southwest and Courtney 10 miles northeast. The Courtney plant was so pubescent that it came as "V. cuspidata" a synonym of V. sororia.

In the fruiting specimen (dried September 19) there are about 15 cleistogamous flowers and fruits; the capsules have matured a few buff seeds, but aborted ovules are far more numerous.

¹ Greene, Pitt. 3: 314, May, 1898.



Hybrid No. 60—Viola nephrophylla \times papilionacea

60. Viola nephrophylla × papilionacea Brainerd.

Plants glabrous throughout; leaf-blades in some plants cordateovate as in V. papilionacea, in other plants reniform as in V. nephrophylla; spurred petal in some plants densely bearded as in V. nephrophylla, in other plants beardless as in V. papilionacea.

Two sets of living plants were sent me, June, 1909, collected by Dr. Ogden of Milwaukee on "original prairie" land in Racine County, southeastern Wisconsin. A specimen from each of these sets was dried September 7, 1909; one, Ogden (No. 3), bore four more or less infertile capsules from petaliferous flowers, seeds olive-brown, and 12 cleistogamous flowers undeveloped; the other specimen, Ogden (No. 4), bore three cleistogamous capsules, all nearly seedless, but showing many aborted ovules.

From the sowing of the seeds of (No. 4) enough fruiting plants were obtained, September 10, 1910, for No. 88 of my Distribution of North American Violets and from seeds of Ogden (No. 3), enough flowering plants for No. 87 of this Distribution.



Hybrid No. 61—Viola nephrophylla imes pedatifida and leaves of parent species

 Viola nephrophylla × pedatifida Brainerd, Bul. Torr. Cl. 40: 259. June, 1913.

V. Wilmattae Pollard, Proc. Biol. Soc., Wash. 15: 178. August, 1902.

Foliage much as in V. papilionacea \times pedatifida, nearly glabrous, palmatifid with several narrow lateral lobes; corolla deep violet, two cm. broad; petals markedly villous and sepals with slight scarious margins, as in V. nephrophylla.

It was not practicable to secure living plants for culture, but both alleged parent species were growing in the canyon (alt. 8,000 ft.) at Beulah, New Mex., 30 miles northeast of Santa Fé, where the type was collected, May 5, 1901, by Mrs. Wilmatte P. Cockerell. The hybrid was again collected by Paul C. Standley in Union County, northeastern New Mexico. The leaf-blades in his specimens in the National Herbarium are cut about half way to the midrib, but on the same sheet are two detached leaves parted as in V. pedatifida, indicating that this species grew with the hybrid.



Hybrid No. 62—Viola nephrophylla imes sororia

62. Viola nephrophylla × sororia Brainerd.

Leaves at petaliferous flowering in May pubescent on petioles and under surface as in V. sororia, not glabrous as in V. nephrophylla; broadly deltoid in August as in V. nephrophylla, not cordate-ovate as in V. sororia.

The hybrid was found in a moist meadow along Cross St., north of the Library, Manchester Center, Vt., October 1, 1906. It was transferred to my garden in Middlebury for study, and herbarium specimens made May 30 and August 3, 1907.



Hybrid No. 63—Viola pallens imes primulifolia

63. Viola pallens × primulifolia Dowell Bul. Torr. Cl. 37: 177, pl. 18. April, 1910.

Freely stoloniferous, pubescent on the peduncles and petioles, about 2 dm. tall. Leaf-blades pale beneath, ovate, acute or obtuse, subcordate to cordate, crenate with low incurved teeth, 4-6 cm. long and $3\frac{1}{2}$ -5 cm. wide in mature leaves, sometimes as wide as long, on petioles about three times as long. White flowers on long slender peduncles equaling or longer than the petioles; capsules green, 5-8 mm. long; seeds small and dark.

The hybrid was collected by Dowell at eight stations on Staten Island, N. Y., through a tract about 12 miles in length. His admirable plate was taken from a plant grown for 14 months in his garden, Dowell (No. 5596).

I have a specimen found by Alvah A. Eaton in an alder swamp, Scabrook, N. H., and sent out from the National Herbarium. It was collected July 2, 1899, but necessarily determined after December, 1905, the date of the publication of *V. pallens*, Rhodora 7: 247.



Hybrid No. 64a—Viola palmata × papilionacea

64. Viola palmata × papilionacea Brainerd Bul. Torr. Cl. 39: 85-88, pls. 5-6. March, 1912. Dowell Bul. Torr. Cl. 37: 177-178. April, 1910.

Leaf-blades cordate-ovate as in V. papilionacea, lobed after the manner of V. palmata, but less deeply so; the capsules from cleistogamous flowers ovoid-conical, 5-7 mm. long, or half as long as the normal capsule in either parent, containing in the 48 capsules examined an average of $4\frac{1}{2}$ seeds to the capsules.

Plants of this hybrid from five stations, and their offspring, have been grown in my garden in Middlebury.

- 1. In June, 1906, Miller sent me from Plainfield, N. J., a plant that he thought to be this hybrid; from this 23 offspring were raised as described above.
- 2. In September, 1905, I detected in the New York Botanical Garden a plant of this hybrid brought in by Miss Angell from Orange, N. J. It was nearly sterile, but from the few ripe seeds obtained plants were propagated for three generations with the same results as in the Miller plant.



Hybrid No. 64b—Viola palmata imes papilionacea

- 3. In the autumn of 1906 I received leaves and a few ripe seeds of a strange plant collected by Miss Pauline Kaufman in the vicinity of New York City. Two generations of its offspring revealed it to be the hybrid here discussed.
- 4. In May, 1909, I saw some excellent photographs of anomalous violets from the wild, taken by Miss Kittredge of Spring Valley, N. Y. One was a glabrous specimen of the normally pubescent *V. palmata*. The plant kindly sent me by Miss Kittredge proved to be quite infertile, only one-fourth of its ovules maturing into seeds. From these were grown plants, some having the deeply lobed leaves of *V. palmata*, others the uncut leaves of *V. papilionacea*.
- 5. On April 15, 1909, similar plants growing with *V. palmata* and *V. papilionacca* were collected at Tryon, N. C., sent home and cultivated with similar results.

In my herbarium are 92 mounted sheets of this hybrid and its offspring.



Hybrid No. 65—Viola palmata × sagittata

65. Viola palmata × sagittata Brainerd, Rhod. 15: 115. June, 1913.

Leaf-blades ciliate and more or less pubescent, subcordate, with 6-8 acute slender lobes chiefly toward the base; capsule infertile.

The hybrid is represented in the Brainerd herbarium by two specimens collected by Dowell, one at Ocean Terrace, Staten Island, N. Y., July 18, 1806 (No. 4518 b); the other at West Orange, N. J., June 22, 1907 (No. 4795). A plant collected by Bicknell at Rosedale, Long Island, N. Y., June 18, 1904, and sent as V. emarginata × palmata, I would call V. palmata × sagittata. I would also place here a plant from Haddonfield, N. J., June 27, 1903 (Stone No. 5138) called V. sagittata.

This, too, is probably the disposition of a still older plant, collected by Ed. S. Denton at Garrisons, N. Y., May, 1886, and characterized by Dr. Gray as "V. palmata towards sagittata."

The plant of Dowell collected July 18, 1806, is the only one seen by me that bears capsules. Their marked infertilty indicates the hybrid character of the plant.



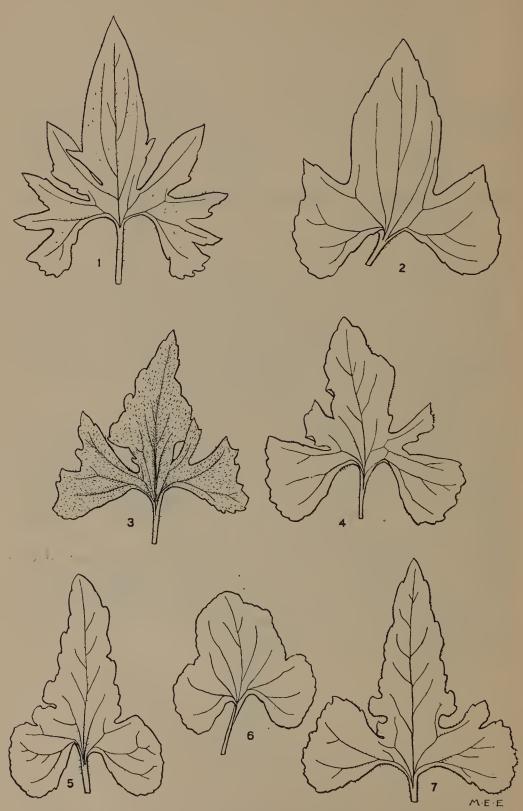
Hybrid No. 66—Viola palmata imes sororia

66. Viola palmata × sororia House Bul. N. Y. St. Mus. (1921) Rpt. St. Bot., p. 53.

Early leaves broadly ovate to reniform, entire or with some of the blades slightly lobed, somewhat pubescent above, glabrous beneath and on the petioles; later leaves softly and rather densely pubescent on the petioles and lower leaf surfaces, the blades less pubescent above, variously 3-7-lobed or nearly entire; flowers abundant, but soon withering without developing fruit; capsules all from cleistogamous flowers on short, horizontal, or deflexed and buried peduncles.

"Saugerties, Ulster Co., N. Y., Peck, May 10, 1904. Type. Also collected at Van Cortlandt Park, New York City, House." In a recent letter House reports that this hybrid is quite common in the Hudson River Valley, where typical *V. palmata* occurs in dry woods on the northern limit of its range. In the neighboring tract of western Massachusetts the most northern known station for the species is Agawam, about 25 miles farther south than Albany, N. Y.

About ten years ago I received from Miss E. Lucy Braun of Cincinnati, Ohio, specimens of an anomalous violet in flower, collected in "dry woods, Hamilton County." With this was sent a drawing of its mature leaves and fruit. The foliage in outline and pubescence is quite the same as in the hybrid here discussed.



Hybrid No. 67—Leaves of Viola palmata \times triloba and of its parents and its offspring

67. Viola palmata × triloba Brainerd, Bul. Torr. Cl. 39: 88-90, pl. 7. March, 1912.

First 1-3 leaves of spring often uncut as in V. triloba, followed by others more or less 5-7-lobed, much like those of V. palmata but the basal lobes broadly dilated and coarsely toothed as in V. triloba; later leaves less dissected, mostly 3-lobed or obscurely lobed; capsule infertile, about one-third of the ovules maturing into seeds; offspring multiform, often bearing on the middle segment of the trilobed leaves 4-8 undulations or coarse teeth.

I have studied four examples of this hybrid, viz.:

- 1. The earliest collection appears to have been that of Miss Angell at Orange, N. J., May, 1900, published by Pollard in Torreya 2: 24, February, 1902, as V. Angellæ.
- 2. A specimen collected June 8, 1903, in Argus, Bucks Co., Pa., by Fretz, published by Stone¹ seems to be this hybrid.
- 3. Among specimens in my herbarium collected by Miss A. M. Ryan in East Lyme, Conn., in 1904 and 1905, are two sheets that I would place here.
- 4. This hybrid was collected in May, 1908, on the Maryland shore of the Potomac River, opposite Harpers Ferry by Greene who named it V. variabilis.² A dozen plants from the type station were grown in my garden in Middlebury and proved, at least in part, to be the hybrid here discussed.

EXPLANATION OF PLATE OPPOSITE

Fig. 1 is a leaf of V. palmata L.
Fig. 2 is a leaf of V. triloba Schwein.
Figs. 3 and 4, leaves of V. palmata × triloba.

Figs. 5-7, leaves of offspring of this hybrid grown from close-fertilized seeds of one plant.

¹ Proc. Acad. Nat. Sci., Phila., p. 677, Dec., 1903. ² Pitt. 5: 90-92, Nov., 1902.



Hybrid No. 68—Viola papilionacea \times pedatifida and two of its segregate offspring

68. Viola papilionacea × pedatifida Brainerd Bul. Torr. Cl. 40: 249-252, pl. 15 Aa. June, 1913.

Rootstock stout, at length extensively branching horizontally; leaves broadly deltoid-ovate in outline cleft into 7-11 linear or oblong lobes, the middle lobe much the widest, glabrous, although the margins are often scabro-ciliolate; petals violet, the odd one more or less villous; cleistogamous flowers on erect or ascending peduncles, intermediate in length between those of the two parent species; capsules 8-12 mm long, infertile, averaging in 12 capsules 8½ seeds; seeds brown, 2 mm long; offspring notably diversiform.

A specimen of this hybrid discovered by Mary O. Pollard, a former pupil, at Yorkville, Ill., May, 1905, was cultivated in Middle-bury for eight seasons. Over 450 offspring extending through four generations were raised, furnishing interesting facts regarding the laws of inheritance in violet hybrids. The principles of Mendelian segregation and reversion were clearly seen to be operative here as in other forms of organic life.

This hybrid seems not to be rare in the Middle West. It has been found in Vinita, Okla., though sent out as V. palmata or V. viarum. From the National Herbarium it has been distributed with printed ticket as V. Bernardi Greene. V. indirisa Greene¹, is doubtless a derivative from of this hybrid.

Several sowings have been made of the seeds of this hybrid; but the ten plants of the first brood (236), whose offspring have been raised for two succeeding generations, are the only ones that will be here discussed. The forms of leaf found in the ten plants and in their respective broods of offspring are presented in the first half of Table I. The second half presents the corresponding facts regarding sixteen offspring of brood 236, plant 3, whose leaf had a hybrid form, quite the same as that of the mother plant from Illinois.

¹ Pitt. 5: 124, pl. 13, Aug., 1903.

CULTURES OF VIOLA PAPILIONACEA X PEDATIFIDA FOR FOUR GENERATIONS

V. papilonacea has leaf uncut:—a V. pedatifida has leaf parted:—A Their Hybrid has leaf cleft:—Aa Ten F ₂ offspring of hybrid 236							Sixteen F ₃ offspring of 236-3							
		Their offspring F ₃								Their offspring—F ₃				
Brood 236	Leaf form	Brood	Number and form		Total	Brood 468		Leaf form	Brood	Number and form			Total	
			A	Aa	а				ł		A	Aa	a	
No. 2	A	595	30		1	30	No.	1	A	605	12	1		12
		(468	6	5	5)	52	No.	2	Aa	606	3	5	5	13
No. 3	Aa	596	8	20	8 }	92	No.	3	Aa	607	4	6	3	13
No. 4	Aa	597	3	6	1	10	No.	4	\boldsymbol{A}	608	14			14
No. 6	a	598			16	16	No.	5	a	609	•		15	15
No. 7	A	599	16			16	No.	6	A	610	20			20
No. 8	Aa	600	1	10	3	14	No.	7	a	611			11	11
No. 9	Aa	601	2	1	1	4	No.	8	A	612	14			14
No. 10	Aa	602	6	6	3	15	No.	9	a	613			16	16
No. 11	A	603	13			13	No.	11	Aa	615	3	6	3	12
No. 12	Aa	604	3	5	2	10	No.	12	Aa	616	3	7	3	13
Total 88 53 39 180				No.	13	A	617	12	}		12			
from Aa's 29 53			23	105	No.	14	\boldsymbol{A}	618	12]		12		
						No.	15	a	619			12	12	
							No.		$\int Aa$	620	2	7	4	13
							No.	17	a	621			14_	14_
							Total			99	31	86	216	
]	From	Aa's.	15	31	18	64

The cultures show that in this hybrid the Mendelian law controls in a general way the inheritance of leaf form, though there is no dominance, the hybrid leaf being intermediate between the leaves of the two parents. The plants that resemble V. pedatifida in having parted leaves always produce offspring with parted leaves; those that resemble V. papilionacca in having uncut leaves always produce offspring with uncut leaves; while those that have the compromise leaf reproduce plants with three forms of leaf incision, as did the original hybrid. Also in the relative number of these forms there is an approximation to the Mendelian ratio 1:2:1. In the above 26 plants (broods 236 and 468), whose forms were verified by their offspring, there are 9 A's, 11 Aa's, 6 a's, the theoretical ratio being: $6\frac{1}{2}$ A's, 13 Aa's, $6\frac{1}{2}$ a's. In the 160 offspring of Aa plants, given above for the third and fourth generations, there are 44 A's, 84 Aa's, 41 a's, the theoretical ratio being: 42½ A's, 84½ Aa's, 42¼ a's. Here we find, as usual, that the larger the number of individuals the closer the normal ratio is realized.

But besides general conformity there are also departures from the strict Mendelian law. For one thing the hybrid or intermediate leaf varies in different individuals, inclining now more to the form of the one parent species and now more to the form of the other. Also the reversionary forms, designated as A and a, are rarely complete reversions. The A plants, though stable in producing like parted leaves in succeeding generations, do not have leaves as deeply parted as in V. pedatifida; and the a plants, though plainly uncut and stable, usually have teeth noticeably longer than in normal V. papilionacea, sometimes even pectinate. (Plate 15, Fig. a.)

Another cause often conspires to increase these differences in leaf pattern: the presence of minor hybrid characters that independently adjust their special conflicts of hybridity. For example, the leaf of V. pedatifida is usually truncate or even cuneate at the base, that of V. papilionacea usually cordate. A hybrid offspring may inherit the broad truncate base of the former with the uncut margin of the latter. Sometimes in the hybrid leaf the lobes are entire, and obtuse at the tip; sometimes, as in the normal leaf of V. pedatifida, the lobes are again cleft or toothed on the outer margin, and acute at the tip.

In these various ways there has arisen in the numerous progeny of the hybrid under discussion a considerable diversity of foliage, such as would present insoluble difficulties to a taxonomic student, who did not know that these diverse forms all came from one individual, by close-fertilized reproduction, in the short period of three or four years. The extreme differences are such as would warrant the making of several distinct species, according to the hasty methods of ordinary practice.

The hybrid *V. papilionacea* × pedatifida seems not to be rare in the Middle West. I cite a few interesting examples: M. A. Castleton 25, Vinita, Okla., April 18, 1891; distributed as "V. palmata." From the United States National Herbarium in 1911 was distributed with printed ticket: "Viola Bernardi Greene, Freeport, Ill., Charles F. Johnson, May 15, 1899; determined by Dr. E. L. Greene and Philip Dowell." The plant is quite the same as the hybrid under discussion from Yorkville, Ill., and seems to represent Dr. Greene's present conception of his species. *V. indivisa* Greene is also a derivative form of this hybrid; the "type" from Prairie Junction, Minn., E. L. Greene collector, July 7, 1898 (Pitt. 5: 124, pl. 13. 1903). Also along railway, Naperville, Ill., L. M. Umbach, May 18, 1897. (Cf. Leaflets 1: 182. 1906).



Hybrid No. 69—Viola papilionacea \times sagittata

69. Viola papilionacea × sagittata Brainerd, Rhod. 8: 54-55. March, 1906.

In general appearance not unlike V. palmata \times sagittata, but glabrous and without lobes; plants often of rank cespitose growth; capsules bearing only half—or even less—the normal number of seeds.

The oldest specimen in my herbarium was collected by Bissell at Southington, Conn. May 28, 1899 and named *V. sagittata*. The hybrid is not infrequent in Connecticut. From the seeds of a plant from Windsor enough specimens were obtained for No. 113 of my Distribution of Eastern North American Violets in 1910.

In June, 1905, Stone sent living plants from Ivy Hill Cemetery, Philadelphia, Pa., and several other collections were made later in the suburbs of that city.

September 7, 1905, I collected the hybrid on a grassy slope near New Brunswick, N. J., growing with both parent species. The plant was so cespitose that only one-tenth of it was needed for a specimen. No capsule contained more than a few seeds, but there were numerous aborted ovules.

In June, 1907, I received from Dowell a living plant collected on Staten Island, N. Y., which developed in the garden the characteristic traits of this hybrid.



Hybrid No. 70—Viola papilionacea \times sororia

70. Viola papilionacea × sororia Brainerd in herb., Dowell Bul. Torr. Cl. 37: 178. April, 1910.

"This differs from V. sororia in having longer petioles, thinner leaves, and less pubescence; while it differs from V. papilionacca in being decidedly more or less pubescent."

Three stations on Staten Island are cited by Dowell.

The 13 sheets of this hybrid in my herbarium are from six different stations:

- 1. Two additional stations in Southeastern New York, namely, Spring Valley, and Stamford, Dowell (5808); the plants from the latter location were so sterile that only 70 seeds were found in four capsules.
- 2. Madisonville, Hamilton Co., Ohio, E. Lucy Braun, collector, April 23, 1911.
- 3. Original prairie, Racine Co., Wis., Ogden, collector; from the offspring of two plants enough specimens were obtained for No. 114 of my Distribution in 1910 of Eastern North American Violets.
- 4. Prairie, Baldwin, Kan., four numbers representing the hybrid in flower and in fruit.
- 5. Greenwood, Mo., Bush, collector, April 25, 1911; specimens ex horto August 17.
 - 6. Mansfield, La., April, 1910; ex horto August 27.



71. Viola papilionacea × Stoneana Brainerd Bul. Torr. Cl. 39: 93. March, 1912.

Glabrous; first one or two leaves uncut, succeeded by larger ones 5-7-lobed; the middle segment broad, the basal lunate coarsely serrate, the lateral but slightly if at all narrowed at the base; autumn leaves often much dilated and obscurely lobed; capsules more or less infertile, 7-12 mm. long; offspring diversiform as to lobation.

A plant of this was taken from Ivy Hill Cemetery, Philadelphia, Pa., September, 1905. From close-fertilized seed collected and sown in the autumn of 1906 were grown the following season, plants that had three distinct leaf forms: (1) the uncut leaf of *V. papilionacea*; (2) the 5-parted leaf of *V. Stoneana* with segments much narrowed toward the base; (3) the 5-lobed leaf of the original plant. From six of these plants a third generation was grown in 1909, in which all from (1) and (2) were homophyllous, and those from (3) heterophyllous, as in the brood obtained in 1907. From (1) a fourth generation was raised in 1910, all like the parent.

72. Viola papilionacea × triloba Brainerd Bul. Torr. Cl. 39: 90-92. March, 1912.

Leaves of late spring and summer shallowly, often obscurely, 3-5-lobed, uncut leaves subcordate, often broadly reniform; capsules



Hybrid No. 72—Viola papilionacea \times triloba

even from cleistogamous flowers infertile; offspring inheriting diversely the opposed characters of the parent species.

My first acquaintance with this hybrid was through some anomalous living plants sent from Washington, D. C., in May, 1906, by Steele, along with samples of pure V. triloba. The six plants of the latter were quite alike—pubescent, cut-leaved, buff-seeded, fertile, and easily separated by the purple tinge of the early spring foliage from the anomalous plants. These were of three forms: (1) One plant fairly fertile, with pubescent uncut leaves as in V. sororia but bearing buff seeds. (2) Two plants fairly fertile, with uncut leaves and dark brown seeds as in V. papilionacea but pubescent. (3) One plant nearly sterile, averaging 6½ brown seeds to a capsule, the leaves glabrous and somewhat 3-lobed. Offspring were raised from all of these: those from (1) and (2), six plants from each, seemed to be stable, that is, in each instance all had characters, like those of the mother; the offspring from (3) were only two, one with uncut leaves, one with 3-lobed leaves.

The problem is to account for the presence in a colony of normal V. triloba of three plants so variant from V. triloba and from each other. But however confused the situation may appear, all may be accounted for by regarding the three odd plants as the descendants of a cross between V. triloba and V. papilionacea, a common species of the region. Plant (1) seems to have escaped the conflict of characters forced into the make-up of the original hybrid and to have attained to stability and relative fertility, inheriting uncut leaves from V. papilionacea but pubescence and buff seeds from V. triloba. Plant (2) seems to be another stable ex-hybrid, inheriting also pubescence from V. triloba but dark brown seeds as well as uncut leaves from V. triloba but dark brown seeds as well as uncut leaves from V. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t. triloba but dark brown seeds as well as uncut leaves from t but t be a common series of the t but t be a common series of the t but t be a common series of the t but t

Some 15 other examples of *V. papilionacea* × triloba might be cited, but I name only two from well known collections: No. 34, North American Violaceae, Greene and Pollard, "*V. palmata dilatata* Ell.", New Springville, Richmond Borough, N. Y., Wm. T. Davis, July 17, 1903; also No. 5108, colony 3, Violets of Philadelphia and vicinity, "*V. palmata dilatata* Ell." Sherwood, Philadelphia, Pa., June 17, 1903. Cf. Proc. Acad., Phila., p. 677, pl. 33, June, 1903.



Hybrid No. 73-Viola pedatifida × sagittata and leaves of its parents and of nine offspring

EXPLANATION OF PLATE

A Leaf of Viola pedatifida Dow, etc.
a Leaf of Viola sagittata Act. pubescent form.
Aa V. pedatifida × sagittata.
The remaining figures show characteristic leaves of nine offspring of the hybrid ex horto Oct., 1909.

73. Viola pedatifida × sagittata Brainerd Bul. Torr. Cl. 40: 252-253, pl. 16. June, 1913.

Plant becoming cespitose, the rootstock dividing into several erect branches; leaves that develop after petaliferous flowering finely pubescent especially beneath and on the upper portion of the petiole, the blades subcordate-ovate in outline (the width about $\frac{2}{3}$ the length), cleft into 6-8 oblong-linear lateral lobes and a broad slightly toothed terminal lobe, the leaves of late summer relatively broader; petals violet, the three lower villous; apetalous flowers and fruit on erect peduncles as long as the petioles; auricles of sepals long and divergent; capsules green, 6-10 mm. long, often quite infertile; seeds intermediate to those of the two parent species in size and color; offspring much unlike each other in foliage, but blades always incised or coarsely toothed toward the base.

This hybrid first attracted my attention in a parcel of violet specimens collected in central Illinois by Mr. V. H. Chase, and sent me in November, 1907, for determination. It was found in undisturbed prairie soil along the right of way of the Rock Island and Peoria Railroad, just north of the south boundary of Stark County. At the same place and time were collected V. pedatifida and pubescent V. sagittata, the three plants bearing the consecutive numbers 1356-7-8. The anomalous plant impressed me as distinct from V. pedatifida \times sororia, discussed below, and as a cross between the two species with which it grew. Mr. Chase, to whom I appealed for living plants, found that the station had been recently burned over; but the following May he discovered another colony along the railway a half mile farther south (V. H. Chase 1619). The stocky specimen sent was easily divided, and six or eight vigorous plants were obtained during the season of 1908. Mr. Chase reported that the pubescent V. sagittata "was very abundant, thousands of plants cover the ground with a blue carpet, mostly where the land was a little low and damp. V. pedatifida seemed to prefer rather drier ground. The hybrid was invariably with V. pedatifida, on fairly dry soil; and V. sagittata was never more than a few rods away."



During the season of 1909 I grew 19 offspring of Chase 1619, and they gave abundant evidence as to the taxonomic status of the mother plant. Leaves of nine of these offspring are figured and indicate something of the marked diversity of form resulting from the combination, in the leaf of the original hybrid, of at least four pairs of opposed characters, that blend or segregate, independently and variously, in the several offspring.

¹ These are: 1. Outline

Outline
 Form of base
 Incision

V. pedatifida
broadly flabelliform
truncate or cuneate
2-3-ternately dissected, i. e.,
The leaf-blade is ternately
dissected two or three
times.
See Bul Torr. Cl. 38:

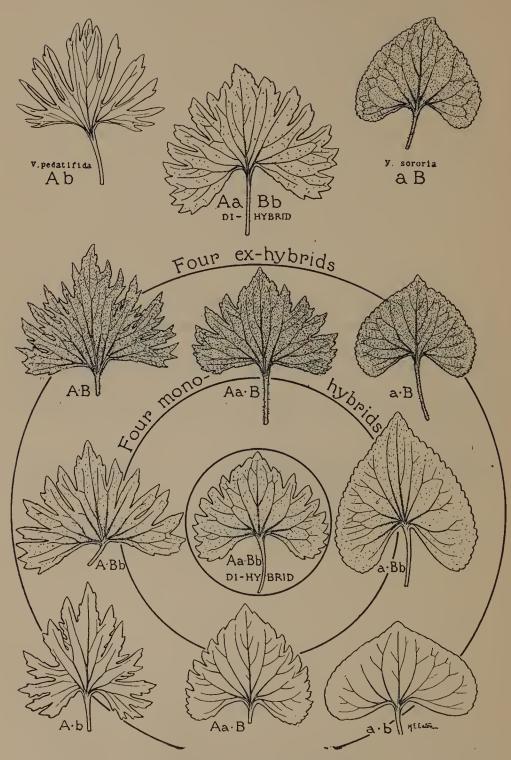
times.

See Bul. Torr. Cl. 38:
6-7. pl. 1, fig. 2, Jan.. 1911.
margins and veins hirtellous

V. sagittata lanceolate cordate or subcordate coarsely toothed at base

finely pubescent

4. Pubescence



Hybrid No. 74, Diagram X—Leaves of Viola pedatifida × sororia, of its parents, and of nine offspring

A.b a reversion to Viola pedatifida a.B a reversion to Viola sororia A.B & a.b new and stable forms

74. Viola pedatifida × sororia Brainerd Bul. Torr. Cl. 40: 253-259, pl. 17. June, 1913.

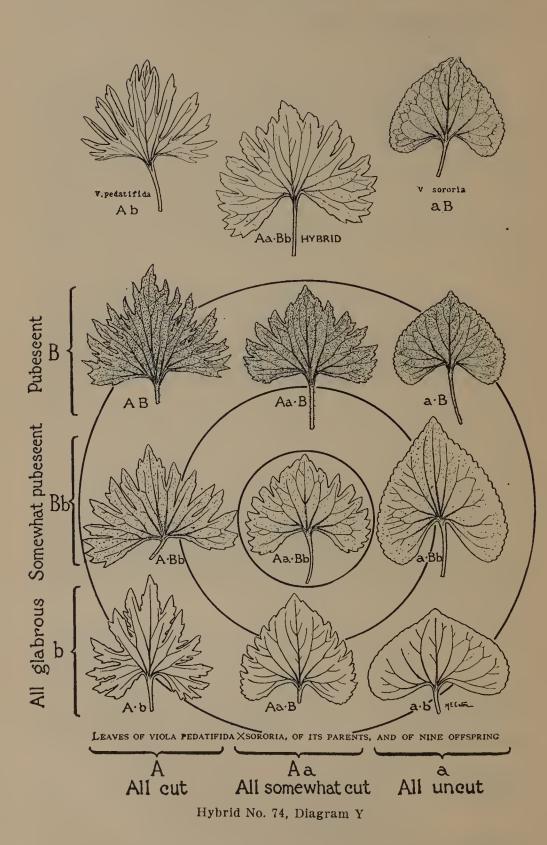
Becoming cespitose with multicipital caudex; leaves that expand at petaliferous flowering 9-13-cleft, the lateral lobes broadly linear, usually with one or two coarse teeth on the outer edge toward the apex, the middle lobe much broader and incised on either side, the upper face somewhat hirtellous, the lower surface and the petioles villous; the leaves of summer larger and less deeply cleft; apetalous flowers on rather short, erect or ascending peduncles; the capsules somewhat blotched with purple, bearing 5-20 brown seeds 2 mm. long; offspring markedly dissimilar. Not rare on prairies of the Middle West.

I am greatly indebted to the kindness and skill of Mr. Chase for the abundant and excellent material used in the study of this hybrid. Collectors in this region know that the native flora of the open prairie is now largely restricted to untilled strips of land along the borders of railways. On May 16, 1909, Mr. Chase, whose bicycle was adjusted to run on rails, traversed in five hours the 24 miles between his home at Wady Petra and the town of Galva. In order to make the return by train, he says, "I could not stop to hunt along the way; but whenever I saw a cut-leaved violet that was not V. pedatifida I stopped for it." The twelve numbers of living plants collected on this trip reached me safely, and all have flourished in the Vermont garden.

The status of hybrid plants in the wild is well shown by a detailed study of these specimens and of their offspring; for all but two sterile plants have been reproduced by seed. The main points regarding them, that have a bearing on the present problem of hybridism, are presented in the following tabular synopsis:

VIOLET PLANTS COLLECTED BY V. H. CHASE IN CENTRAL ILLINOIS, MAY 16, 1909

	Chase's herb. no.	Leaf characters		Capsule color	Seed color	Av. no. in one capsule
V. pedatifida Don	\[\frac{1951}{1956} \]	(parted)	b (glabrous)	(green)	d (buff)	70
V. sororia Willd	1291	a (uncut)	B (villous)	(purple)	D (brown)	66 (glabrous)
V. papilionacea Ph.	1958	a	b	C	D	66
-	1950	Aa	Ъ	sterile		0
V. papilionacea	1952	a	b	c	Dd	7
× pedatifida	1949	Aa	Ъ	Cc	d	$9\frac{2}{3}$
pountificati	1947	Aa	<i>b</i> •	Cc	$\left\{egin{array}{l} Dd, ext{ or } \ d \end{array} ight.$	5
<u></u>	1957	Aa	Bb	ste	rile	0
	1955	A	Bb	Cc	Dd	101/2
V. pedatifida {	1953	Aa	Bb	c	Dd	7
× sororia	1954	Aa	Bb	Cc	Dd	8
· ·	1948	Aa	Bb	Cc	Dd	18



Nos. 1951 and 1956 are *V. pedatifida;* and I have added to the list, though not collected May 16, 1909, *V. sororia*, the other parent of the hybrid under discussion; specimens of this had been previously sent me by Mr. Chase from four stations in his vicinity. No. 1958 is the prairie form of *V. papilionacea*, named *V. pratincola* by Dr. Greene (Pittonia 4: 64. July, 1899). These three are common and widespread species of the Prairie States from Canada to Texas; the first and third reach westward to the mountains of Colorado.

Four of the numbers are the hybrid V. papilionacca imes pedatifida already discussed in this paper. Of these No. 1950 flowers freely in May with showy flowers, that often appear also in July and August; but apetalous flowers are rare, and neither sort has been found to produce seed. The three others are also nearly sterile, bearing only 5-10 seeds to a capsule; but none of the three turns out to be like the Pollard plant from Yorkville in being a first cross (or F1), the form to be selected as the starting point for experiments on the laws of inheritance in hybrid offspring. No. 1952 has an uncut leaf as in V. papilionacea and a green-colored capsule as in V. pedatifida, both recessive or reversionary-characters never found in a first cross. No. 1949, on the other hand, has the hybrid leaf and the hybrid capsule color but the buff seeds of V. pedatifida and is therefore another sub-hybrid. No. 1947 consists of five plants, the seeds of which differ in color, and the leaves of which, though somewhat incised, display at least three unlike patterns; the five plants therefore must be considered the offspring of an earlier hybrid.

The remaining plants of the 1909 collection are equally variant forms but of V. pedatifida \times sororia. No. 1957 is of dwarf habit and has the compromise or hybrid leaf; but though vigorous and multiplied by division into eleven plants, it has failed to yield a single seed. No. 1955 (six plants by division) has a leaf more deeply cut that the others, and this style of leaf reappears in all its offspring. In this we see a reversion, far from complete but stable, to the leaf of V. pedatifida. No. 1953 (again six plants by division) has the pure green capsules of V. pedatifida, as have also its offspring, and so is another sub-hybrid. But the two remaining numbers, 1954 and 1948, seem to be the desired first product of hybridism, all the four pairs of opposed characters in the double parentage appearing in a compromise form in both numbers. A flowering specimen of 1954 was distributed in my "Violets of Eastern North America, 1910," No. 121; and in No. 122 are shown two sister offspring, one with the uncut leaves of V. sororia, the other with the

parted leaves of *V. pedatifida.*¹ No. 1948, being unusually fertile for a hybrid, was chosen for the basis of a somewhat detailed study of the reproductive behavior of a tetrahybrid.

During the season of 1910 twenty-one plants were grown from the seeds of Chase 1948. In August nearly all bore cleistogamous flowers. which matured several capsules of seeds. These were sown about December 1 in shallow boxes and placed in a cold frame with no protection from the winter weather but a covering of burlap. In the spring of 1911 all but seven of these sowings gave broods of F₃ offspring, containing each 6-18 plants. These have been carefully observed for two seasons and the characters of each plant noted as respects leaf incision, pubescence, color of capsule, and color of seed, four qualtities in which the parent species were opposed. In each of these four qualities the plant resembled either V. pedatifida, V. sororia, or their hybrid; and in most instances the data were at hand, and clear enough, to determine at once this resemblance by inspection. In the case of the sixteen F; plants of brood 781, here made use of, the characters were verified by the behavior of their offspring, the reversionary forms alawys proving stable, the hybrid forms always unstable. The details of this experiment are given in table III, in which the symbols Aa, Bb, Cc, Dd denote the blend or hybrid character.

The statements made above regarding the marked diversity of leaf pattern in the offispring of V. papilionacea \times pedatifida and the departures from strict Mendelian law are equally true of the analogous hybrid V. pedatifida \times sororia. The imperfect reversions in leaf form are shown in Plate 17, Fig. A.B, A.Bb, and A.b. compared with the leaf of V. pedatifida figured above them. But in this hybrid the same phenomena are observable also in the varying colors of capsule and of seed. In all three pairs of characters the stable reversions marked A, C, and D are not complete reversions. The darkest capsule or seed found in the F_2 brood is much lighter than the capsule or seed of V. sororia.

It is further to be observed that though the Mendelian law leads us to expect on the average one of each of these reversions in every four offspring, we have here only one of each in the sixteen offspring. At the same time the hybrid forms are in excess of the normal average

¹ In one of our large herbaria, where the work of mounting is done by novices, these two offspring were considered too unlike to appear on the same sheet. Only the plant with uncut leaves was mounted over ticket 122; while the sister plant with parted leaves was placed on the sheet with No. 121, which indeed it more closely resembled. That two plants so dissimilar should come from one self-fertilized parent has seemed incredible even to certain "botanists."

(one-half of the whole number); instead of 8 of each we have 10 Aa's, 12 Cc's, and 10 Dd's. And it should be remembered that this statement is not based solely on the appearance of the F_2 plant but on the fact that the reversionary characters, A, C, D, were found to be stable in reproduction; while the hybrid characters were found to be unstable. For example, with the exception of No. 4, which had only two offspring, each of the ten Aa plants in brood 781 gave 2-7 plants with uncut leaves.

VIOLA PEDATIFIDA X SORORIA, CHASE 1948, AND ITS OFFSPRING

Hybrid F,	Aa	Bb	Cc	Dd			
forms of sixteen F2 offspring					F ₈ offspring of brood 781		
Brood	Folia	age	Cap sule	Seed	Brood	Size	Exhybrids
781 No. 1	a	В	Cc	d	853	13 plants	$8 \left\{ \begin{array}{l} 5 & a.B.C.d \\ 3 & a.B.c.d \end{array} \right.$
781 No. 3	a	B	Cc	d	855	10 plants	$7 \left\{ \begin{array}{l} 2 a.B.C.d \\ 5 a.B.c.d \end{array} \right.$
781 No. 4	Aa	Bb	Cc	Dd	856	2 plants	0
781 No. 6	A	Bb	Cc	Dd	858	16 plants	$egin{array}{c} 3 \left\{ egin{array}{ccc} 1 & A.B.c.d \ 1 & A.b.C.d \ 1 & A.b.c.d \end{array} ight. \end{array}$
781 No. 7	Aa	b	Cc	Dd	859	7 plants	0 (1 21.0.0.0
781 No. 8	Aa	B	C	d	860	6 plants	$egin{array}{c} 4 egin{array}{ccc} 2 & a.B.C.d \ 2 & A.B.C.d \end{array}$
781 No. 9	Aa	B	Cc	D	861	16 plants	$3 \begin{cases} 1 & A.B.C.D \\ 1 & A.B.c.D \end{cases}$
781 No. 10	Aa	b	Cc	Dd	862	14 plants	$egin{array}{cccc} 1 & a.B.c.D \ a.b.c.D \end{array}$
781 No. 11	Aa	Bb	c	Dd	863	11 plants	$egin{array}{c} 2 \left\{ egin{array}{ccc} 1 & A.b.c.d \ 1 & a.b.c.d \end{array} ight. \end{array}$
781 No. 13	a	Bb	Cc	Dd	865	2 plants	0
781 No. 14	a	B	c	Dd	866	9 plants	$\begin{array}{c} 6 \begin{cases} 3 & a.B.c.D \\ 3 & a.B.c.d \end{cases}$
781 No. 15	Aa	Bb	C	d	867	15 plants	$\frac{1}{a}$ a.B.C.d
781 No. 16	Aa	Bb	Cc	Dd	868	10 plants	0
781 No. 17	Aa	Bb	Cc	d	869	18 plants	$ \begin{array}{c} 2 \left\{ \begin{array}{c} 1 & a.B.C.d \\ 1 & a.B.c.d. \end{array} \right. \end{array} $
781 No. 19	a	b	Cc	Dd	871	8 plants	$egin{array}{cccc} 1 & a.b.c.d \ 1 & A.b.C.d \end{array}$
781 No. 20	Aa	b	Cc	Dd	872	14 plants	$\left \begin{array}{c}1&A.b.c.d\\1&A.b.c.d\\1&a.b.c.d\end{array}\right $
						171 plants	 41

And not only in the second but also in the third generation of this hybrid the number of plants having the positive character seems to fall short of the Mendelian requirements. This appears if we note the ratio in which the several hybrid characters in brood 781 segregate in the F_3 offspring:

```
The 10 Aa plants had 113 offspring: 23 A's, 54 Aa's, 36 a's
The 7 Bb plants had 74 offspring: 14 B's, 35 Bb's, 25 b's
The 12 Cc plants had 130 offspring: 23 C's, 67 Cc's, 40 c's
The 10 Dd plants had 93 offspring: 13 D's, 44 Dd's, 36 d's

\begin{cases}
20:48:32 \\
19:47:34 \\
18:51:31 \\
14:47:39
\end{cases}
```

Total 410 73 normal ratio: 25:50:25

Combining these results, we find in 410 instances of the reproduction of a hybrid character, that instead of $102\frac{1}{2}$ reversions to the positive character there are only 73; instead of 25 percent, only 18.

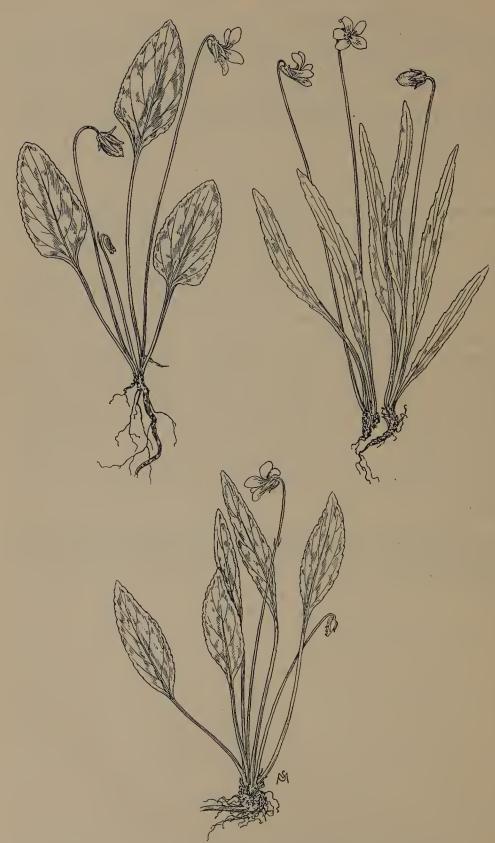
However, the determination of the characters in these 171 F₃ offspring rests only upon their appearance, having not been as yet verified by observing the behavior of the F₄ offspring. Of this generation 45-50 broods are hoped for by another season from seed already sown. But we seem to be already justified in the suspicion that in a specieshybrid as complex as the one under experiment, where the opposed characters of the parents appear in a blend or intermediate form, this form may acquire a certain degree of fixity, whereby the reversions to the positive type in a pair of opposed characters are less complete and less frequent than in normal Mendelian segregation and the reversions to the negative type more frequent. If we might assume that the gametes holding the positive character were more or less impure, while the gametes holding the negative character were pure, the situation would be fairly well accounted for.

In the great diversity of forms displayed in the 171 F₃ offspring the most interesting group are the 41 exhybrids, in which all of the four characters under study are reversionary and constant. Among these we find three plants in which the four characters of *V. pedatifida*, *A.b.c.d*, reappear, one plant in each of the broods 858, 863, and 872. What may be called a form of *V. pedatifida* with uncut leaves, *a.b.c.d*, is found once in each of the broods 863, 871, 872. A pubescent *V. pedatifida*, *A.B.c.d.*, occurs in brood 858. A purple-capsuled *V. pedatifida*, *A.b.C.d*, occurs in both 858 and 872. Similarly, we have a cutleaved *V. sororia A.B.C.D*, in brood 861; a green-capsuled *V. sororia*, *a.B.c.D*, once in brood 861 and three times in brood 866; and a buff-seeded *V. sororia*, *a.B.C.d*, in broods 853, 855, 860, 867, and 869, eleven plants in all. In short, all but five of the sixteen possible combinations in fours, of these eight pure elementary characters, are to be found in these 41 plants.

As showing how a hybrid tends in successive generations to eliminate its hybrid characters, ever becoming simpler and finally pure, we note that starting with the F₁ plants, necessarily hybrid in all the opposed characters of the two parent species, we have in the next generation only two such hybrids, and in the 171 plants of the 3d generation, none; indeed, the law of probability calls here for only one in every 256 offspring.

My first recognition of V, pedatifida \times sororia was in a package of living plants sent May 22, 1907, by Dr. H. V. Ogden of Milwaukee, collected at Upper Nemahbin Lake, Wis., growing with both parents, and considered by him as "doubtless a hybrid," The same thing, however, had been sent me some three years earlier by Dr. Greene as a specimen of his V. Bernardi, collected by himself at Dixon, Ill., June 18, 1898. In Leaflets 1: 184, January, 1906, the plant is transferred to V. perpensa, then first described. I have recently examined the three other specimens there cited and regard them all as forms of V. pedatifida × sororia.¹ Also V. fallacissima Greene, Leaflets 1: 185. February 24, 1906, is another form of the same hybrid from western Missouri—Bush 141, Lee's Summit, Mo., July 8, 1899. Other specimens are: E. J. Palmer Nos. 3345 and 3393, Webb City, Mo., April 19 and May 5, 1911; Mary O. Pollard No. 6, Yorkville, Ill., May 16, 1909; L. M. Umbach, prairies, Clarenden Hills, Ill., June 21, 1899—distributed in 1911 from United States National Herbarium as "V. balmata."

¹ I therefore wish to correct my statement in Bul. Torrey Club 37: 584. 1910 that *V. perpensa* Greene is the western form of *V. palmata*—a too hasty inference from the fact that a *V. palmata* specimen in my herbarium from Aurora, Ill., was once named *V. Bernardi* by Mr. C. L. Pollard. See footnote in Bul. Torr. Cl. 40: 25-9, June, 1913.



Hybrid No. 75—Viola primulifolia \times vittata and parent species

75. Viola primulifolia × vittata Brainerd, hyb. nov.

Plants stoloniferous; petals white, the three lower striped with dark lines; leaves 6-10 cm. long at petaliferous flowering, the blades narrowly lanceolate decurrent on the petiole, obscurely crenate-serrate as in *V. primulifolia*, and mucronately serrulate as in *V. vittata*.

Boggy edges of "ti-tı swamp," Chickasaw, Mobile, Ala., Miss Cecile Sheppard collector, March 20, 1923.



Hybrid No. 76—Viola rosacea \times sagittata

76. Viola rosacea × sagittata Brainerd.

Leaf-blades usually intermediate in outline between V. rosacea and V. sagittata, often hastately cleft at the base, usually much wider than in V. sagittata; the under surface glabrous, the upper more or less hirtellous as in V. rosacea.

This hybrid was first found in flower on the fair grounds, Crowley, La., March 25, 1910, growing with both parent species. Plants transferred to my garden in Middlebury furnished fruiting specimens the following October. Seedling of the hybrid gave reversionary forms: some with uncut blades as in *V. rosacea*, others with hastately cleft, deltoid blades as in the parent hybrid; seeds buff as in *V. rosacea*, not brown as in *V. sagittata*.



Hybrid No. 77—Viola rostrata \times striata

77. Viola rostrata × striata Brainerd, hyb. nov.

Outline of leaf-blade broadly ovate-cordate, acuminate; stipules slightly fimbriate as in V. rostrata; like V. striata in its thick, short, blunt, spur and bearded lateral petals.

I am indebted to Miss E. Lucy Braun of the University of Cincinnati, for specimens of this hybrid collected May 27, 1917, and May 26, 1918, near Terrace Park, Hamilton Co., Ohio. With these were also specimens of V. striata collected at the same time and place. Miss Braun, at her first discovery of the plant, was driven away by a violent thunder-storm, and the plants collected she took to be V. rostrata.

A year later she revisited the station and found that she had collected not only the hybrid, but the two parent species. A specimen of the earlier collection transferred to her garden bore cleistogamous flowers abundantly, but failed to produce any seed.



Hybrid No. 78—Viola sagmata × sororia

78. Viola sagittata × sororia Brainerd, hyb. nov.

Plants varying in leaf-outline from ovate with crenate-serrate margin, as in *V. sororia*, to lanceolate with hastate basal lobes, as in *V. sagittata*; varying also in like manner as respects other characters that differentiate the parent species.

These anomalous plants were first found by Dr. Ogden of Milwaukee, Wis., growing in a moist, partly shaded meadow in Nashotah, about 17 miles west of his home. Five living plants, differing more or less from each other, were sent August 10, 1906, and grown with their offspring during the following four years. Samples were distributed in 1910 as Nos. 142 and 143 of my Violets of Eastern North America.

We seem to have here an instance of Mendelian segregation. An original cross has borne offspring for several or many generations that present a diversiform recombination of the parental characters. Nature has only been doing what breeders of plants have learned to do with notable success.



Hybrid No. 79—Viola sagittata \times triloba

79. Viola sagittata × triloba Brainerd, hyb. nov., Rhod. 8: 54, March, 1906, as amended Rhod. 15: 115. June, 1913.

Differing from V. sagittata in having wider pubescent leaf-blades more or less lobed near the middle, in having cleistogamous flowers with appressed ciliate auricles, and in having a brown-spotted summer capsule on much shorter peduncles; differing from V. triloba in having ovate-oblong leaves with coarsely toothed or incised basal lobes, and in having long slender cleistogamous flowers on ascending peduncles; in each case the difference being in the direction of qualities possessed by the other parent.

This hybrid was collected by House and Eggleston June 12, 1904, near New Brunswick, N. J., growing not far from both parent species; the fruit in autumn was nearly sterile, bearing only 19 seeds in the four capsules examined.



Hybrid No. 80—Viola septentrionalis \times sororia

80. Viola septentrionalis × sororia Brainerd Rhod. 6: 221. Nov., 1904.

Differs from V. sororia in having a narrower leaf-blade, finer pubescence and a villous spurred petal; from V. septentrionalis in having less ciliolate sepals; from both in being extremely sterile.

Only one station for this hybrid was known when it was published in 1904. This was a narrow terrace of fine silt between the river and the railway south of Middlebury, Vt., in a colony of V. sororia and not far from plants of V. septentrionalis. The hybridity and parentage of the plant were unmistakable.

Subsequently a fine station for the hybrid was found along the outlet of a cold spring at the base of the mountain in northeastern Middlebury. Plant transferred to the home garden and their offspring were under observation for five years. It is No. 157 in my Distribution in 1910 of Eastern North American Violets.



Hybrid No. 81—Viola sororia × triloba

Viola sororia × triloba Brainerd Bul. Torr. Cl. 39: 92-93. March, 1912.

The confluence of these two species is generally recognized, and it is so common that many students of Viola have regarded them as forms of the same species; just as, because of a similar confluence, V. sagittata has been held to include V. fimbriatula. The shallow and obscure lobes of the hybrid leaf are the same as in V. $papilionacea \times triloba$, but the foliage is never glabrous. But more satisfactory than this negative test is the discovery of the intermediate forms in a region from which V. papilionacea is absent. Along a shady limestone ledge in Orwell, Vt., where V. triloba and V. sororia were abundant, but no V. papilionacea, was found in 1904 a large colony of intermediates that will pass muster as V. $sororia \times triloba$. In this case the most satisfactory evidence would come from the artificial production of the hybrid. This is now under way at this station.

It may be noted that the leaf outline in V. triloba is relatively broader and less deeply cordate than in V. sororia (or in V. papilionacea), and that the hybrid offspring may inherit the uncut leaves of the latter and the broad outline of the former, thus presenting a decidedly reniform leaf. Such stable forms often emerge in experimental cultures and in the wild are occasionally met with near stations for V. triloba. I have usually found such broad-leaved specimens of "V. sororia" to be infertile. It seems to be this that Greene has named V. populifolia.

¹ Pitt. 3: 337, Sept., 1898.



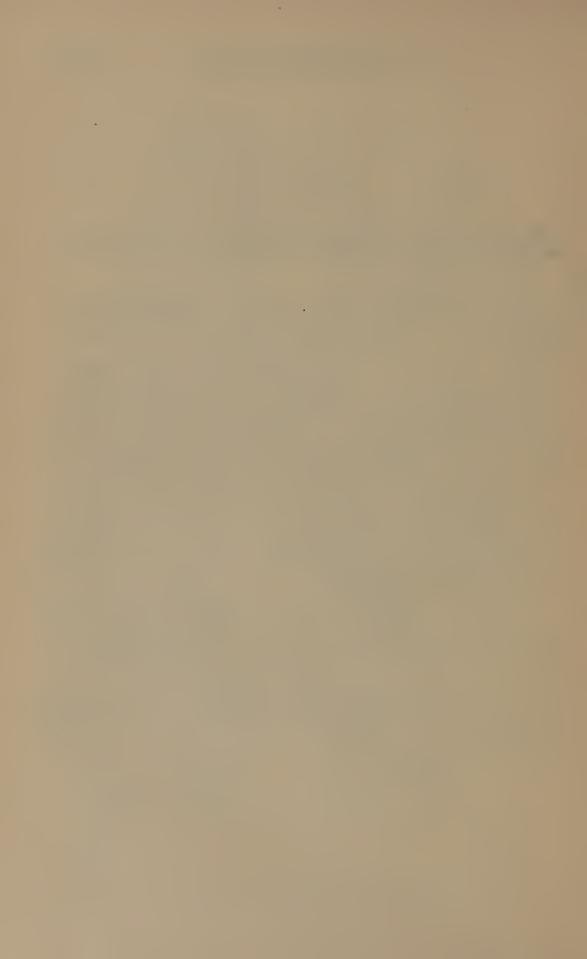
Hybrid No. 82—Viola Stoneana \times triloba

82. Viola Stoneana × triloba Brainerd Bul. Torr. Cl. 39: 93-94. March, 1912.

Leaves 5-lobed; lower surface and petioles somewhat pubescent; capsules infertile; seeds buff; offspring in part glabrous, in part quite pubescent.

The original plant was collected at Ivy Hill Cemetery, Philadelphia, Pa., in 1905, with V. papilionacea \times Stoneana. Four seedlings were grown in 1907; one quite glabrous, in this reverting to V. Stoneana; the other three more or less pubescent. From each of the four plants offspring were obtained in 1909. Those from the glabrous plant were also all glabrous; two of the pubescent plants bore both pubescent and glabrous offspring; the remaining pubescent plant bore nine offspring, all pubescent, thus indicating that in this instance the pubescence of the mother plant was a stable character. This happens to be exactly the relative number of these three forms of offspring required, on the average, by the laws of Mendel.

A specimen of this hybrid, House (No. 130) Washington, D. C., July 29, 1904 has an instructive history: It was first named V. palmata L., fide Greene. It was afterward considered by House to have "the cut of V. septemloba Stone but to be as pubescent as V. palmata." We would now substitute V. Stoneana for "V. septemloba Stone," and V. triloba Schwein for "V. palmata L." House correctly surmised the status of the plant, but used the invalid names prevalent before April, 1912.



INDEX OF VIOLET SPECIES AND SOME NATURAL HYBRIDS

Roman type indicates species described in Bull. 224 of this Station to which paging refers.

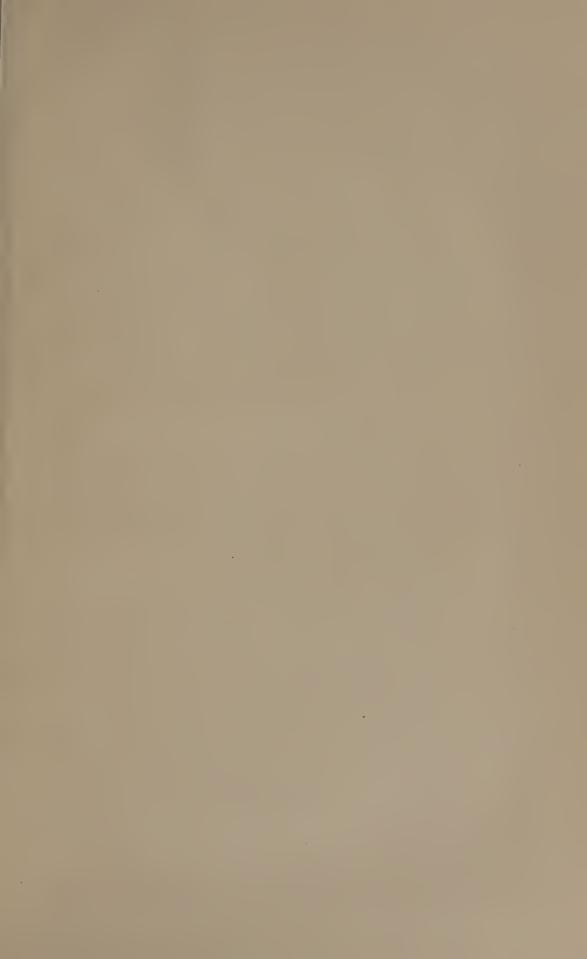
Italies indicate natural hybrids described in this bulletin.

Viola adunca	157	V. emarginata × affinis	23
$V. \ adunca \times conspcrsa$	17	\times Brittoniana	51
V. affinis	49	× fimbriatula	91
V. affinis × Brittoniana	19	imes Lovelliana	93
\times cucullata	21	imes papilionacea	95
\times emarginata	23	\times sagittata	97
imes fimbriatula	25	\times septemloba	99
\times hirsutula	27	\times sororia	101
\times nephrophylla	29	× Stoneana	103
\times palmata	31	V. eriocarpa	131
imes papilionacea	33	V. esculenta	25
\times sagittata	35	V. fimbriatula	63
\times septentrionalis	41	V. fimbriatula \times affinis	25
\times sororia	43	\times Brittoniana	53
$\times triloba$	45	\times cucullata	66
V. Beckwithii	117	\times emarginata	91
V. biflora	101	\times hirsutula	105
V. blanda	81	imes latiuscula	107
V. Brittoniana	69	\times palmata	108
$V. \; Brittoniana \times affinis$	19	imes papilionacea	111
\times cucullata	19	\times sagittata	11 3
	51	× septentrion-	446
× emarginata		alis	115
\times fimbriatula	53	\times sororia	117
× lanceolata	55 57	$\times triloba$	119
\times papilionacea	57	V. Flettii	145
\times sagittata	59	V. floridana	32
× sororia	61	V. glabella	129
imes triloba	63	V. Hallii	119
V. canadensis	137	V. hastata	123
V. chalcosperma	53	V. hirsutula	42
V. chrysantha	113	$V.\ hirsutula imes affinis$	27
V. conspersa	149	× fimbriatula	105
$V.\ conspersa\ imes\ adunca$	17	× palmata	121
\times rostrata	65	imes papilionacea	123
V. cucullata	57	× sororia	125
$V. \ cucullata \times affinis$	21	× Stoneana	127
\times Brittoniana	47	$\times triloba$	129 159
× fimbriatula	66	V. Howellii	79
\times nephrophylla	69	V. incognita	151
$\times palmata$	71	V. labradorica	91
$\begin{array}{c} \nearrow parmata \\ \times papilionacea \end{array}$	73	V. lanceolata	55
$\begin{array}{c} \nearrow paptitonacca \\ \times primulifolia \end{array}$	75	V. lanceolata × Brittoniana	131
$\stackrel{ imes}{ imes} sagittata$	79	× pallens	133
\times saginata \times septentrionalis	81	× primulifolia	161
$\times septemmonants \\ \times sororia$	83	V. Langsdorfii V. Langloisii	51
	87	$V. \ Langlois ii \times rosacea$	135
$igsim imes triloba \ igsim viarum$	89	V. Langioisti × 70suceu V. latiuscula	$\frac{133}{27}$
	143		$\frac{27}{107}$
V. cuneata	143	$V.\ latiuscula \times fimbriatula \ imes sororia$	137
V. Egglestonii	67	$ imes sororia \ imes triloba$	139
V. emarginata	0.7	× 1711000	100

			77.0
V. lobata	125	V. renifolia	76
V. Lovelliana	35	V. reptans	155
V. Lovelliana \times emarginata	93	V. rosacea	29
\times papilonacea	141	V. rosacea × Langloisii	135 189
V. Macloskeyi	85	× sagittata	163
V. missouriensis	31	V. rostrata	65
V. missouriensis × sororia	143	V. rostrata × conspersa	191
V. nephrophylla	54	× striata	95
V. nephrophylla × affinis	29	V. rotundifolia	135
\times cucullata	69	V. rugulosa V. sagittata	64
imes papilionaced		v. sagittata V. sagittata × affinis	35
imes pedatifida	147	\times Sugittata \times agints \times Brittoniana	59
× sororia	149	× cucullata	79
V. novae-angliae	46	× emarginata	97
V. Nuttallii	103	× fimbriatula	113
V. occidentalis	89	\times palmata	157
V. ocellata	141	$\times parmata \\ \times papilionacea$	167
V. orbiculata	97	$\times paptitonacea \ imes pedatifida$	175
V. pallens	82	× rosacea	189
$V.$ pallens \times lanceolata	131	× sororia	193
imes primulifolia	151	$\times triloba$	195
V. palmata	19	V. sarmentosa	99
$V. \ palmata \times affinis$	3 1	V. scopulorum	139
\times cucullata	71	V. Selkirkii	73
imes fimbriatula	108	V. septemloba	72
\times hirsutula	121	$V. \ septembola \times emarginata$	99
\times papilionacea	153	V. septentrionalis	44
\times sagittata	157	$V.$ septentrionalis \times affinis	41
\times sororia	159	× cucullata	81
$\times triloba$	161	× fimbriatul	a
V. palustris	75		115
V. papilionacea	22	imes sororia	197
V. papilionacea × affinis	33	V. Sheltonii	115
× Brittoniana	57	V. sororia	41
× cucullata	73	$V. \ sororia \times affinis$	43
× emarginata	$\begin{array}{c} 95 \\ 111 \end{array}$	\times Brittoniana	61
$ imes \mathit{fimbriatula} \ imes \mathit{hirsutula}$	$\frac{111}{123}$	\times cucullata	83
$\times Lovelliana$	141	\times emarginata	101
\times nephrophyllo		× fimbriatula	117
~ nephi opitytte	145	$\times hirsutula$	125
× palmata	153	× latiuscula	137
× pedatifida	1 63	× missouriensis	143
× sagittata	167	\times nephrophylla	149
× sororia	169	× palmata	159
× Stoneana	171	× papilionacea	169
× triloba	171	× pedatifida	179
V. pedata	15	× sagittata	193
V. pedatifida	71	$igsim imes ext{septentrionalis} \ igsim imes ext{triloba}$	197
V. pedatifida × nephrophylla	147	V. Stoneana	199
× papilionacea	163		21
× sagittata	175	$V. \ Stoneana \times emarginata \ \times \ hirsutula$	$\begin{array}{c} 103 \\ 127 \end{array}$
× sororia	179		
V. pedunculata	102	$ imes papilionacea \ imes triloba$	$\begin{array}{c} 171 \\ 201 \end{array}$
V. praemorsa	107	V. striata	147
V. primulifolia	87	$V. \ striata \times rostrata$	191
V. primulifolia × cucullata	75	V. triloba	37
× lanceolata	133	$V. triloba \times affinis$	45
× pallens	151	\times Brittoniana	63
$\times vittata$	187	× cucullata	87
V. pubescens	131	× emarginata	91
V. purpurea	109	× fimbriatula	119
V. Raffinesquii	164	× hirsutula	129

		Some Natura	AL VIOLET HYBRIDS	205
V.	triloba × latius	scula 139	V. tripartita	127
	× palm	ata 161	V. viarum	61
	\times papil	lionacea 171	V. viarum > cucullar	ta 89
	\times sagit		V. villosa	61
	× soror	ria 199	V. vittata	93
	× Stone	eana 201	$V. \ vittata \times primuli$	folia 187
v.	trinervata	121		153









Date Due					
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8					







